ECOLOGY OF THE ARID AND SEMI-ARID AREAS OF THE UNITED STATES AND CANADA

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ARID ZONE PROGRAMME

A report on the Ecology of the Arid and Semi-arid Areas of the United States and Canada

prepared for Unesco

By

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INTRODUCTION

This review is aimed toward providing basic information on results obtained and principles derived from research in plant ecology in the arid and semi-arid areas of the United States and Canada. It is hoped that this material will be of interest and value in similar regions throughout the world.

Because of space limitations, it was possible to include only a part of the publications in plant ecology and closely allied economic phases, such as, range ecology, afforestation, and the development of adapted crops from native species. Even so, it is believed that the bibliography accompanying this report is representative of the available literature. In fact, the titles included in this report were selected from about three times their present number. This selection was made on the basis of importance and distribution, with an effort to have representative coverage by subject matter and by geographic areas.

The very broad nature of the material covered in this review brings up some questions as to how it might be arranged and organized to the best advantage in the interests of usability and readability. At first, it was planned to present the material in an orthodox ecological arrangement with the discussion of factors segregated from the discussion of autecological and phytosociological reactions. But, as the available material was reviewed, it was found that a more coherent presentation with less repetition could be obtained by making certain combinations. Working these out on the basis of discussing the most closely related subjects in sequence, the review has been organized as outlined below:

I. Brief discussion of the physical features of the arid and semi-arid areas
   - A. Climate
   - B. Physiography
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It is regretted that animal ecology could not be included in this review. As Dice (157) has pointed out, the native fauna is certainly as closely associated with the vegetation as the domestic animals whose influence is covered in the discussion of grazing. Certainly, on this basis, it would be logical to include the wild animal life and to make the discussion bio-ecological in scope. However, bringing in animal ecology on anything like an adequate scale would enlarge the amplitude of this report beyond reasonable limits; so the animal phases have been left for some future review. In the meantime, the excellent texts with comprehensive bibliographies, such as, Bio-ecology by Clements and Shelford (115) and Principles of animal ecology by Allee et al (16) will provide basic information for those interested in the bio-ecology of arid and semi-arid areas.

PHYSICAL FEATURES OF THE ARID AND SEMI-ARID AREAS

There is fairly general agreement as to what constitutes the overall arid and semi-arid areas of the United States and Canada. Numerous investigators (1, 66, 111, 112, 124, 250, 280, 294, 298, 314, 350, 404, 415, 505, 506, 507, 535, 548, 549, 551, 552) have suggested various systems and schemes based on climate,soils, and vegetation to delineate "semi-arid" and "arid" areas. While they have differed among themselves as to the value of the various criteria, there is no major difference among them in setting up regional limits except, possibly, in the location of the boundary line along the broad eastern transitional zone between sub-humid and semi-arid. This semi-arid region, which includes within its boundaries the arid area, lies in the western part of the United States and Canada. One major portion lies mostly in

the Great Plains region east of the Rocky Mountains, and a second portion lies largely within the basins between the Rocky Mountains and the Pacific humid belt.

Thornthwaite (505) set the boundary separating sub-humid and semi-arid on the basis of his P-E index (precipitation over evaporation) between values of 31 and 32. On this basis, the eastern boundary in the United States lies approximately along the 101st meridian. This line cuts North Dakota and South Dakota a little west of centre and includes within the semi-arid area the western one-fourth of Nebraska and Kansas, most of the Panhandles of Oklahoma and Texas, and continues southward to the Gulf of Mexico near Corpus Christi, Texas. Later, Thornthwaite (507) modified his scheme of classification to take into consideration potential evapo-transpiration, but this did not materially change the boundaries of his climatic provinces. Shantz (442) considered the eastern boundary line between the 99th and 101st meridians on the basis of vegetation, while Marbut (307) was inclined to consider the 101st meridian as more nearly the dividing line. Among the earlier workers, Vasey (534) placed the eastern boundary of the "arid" region at the 100th meridian.

In Canada, the eastern boundary of the semi-arid province begins at a point just east of the south-east corner of Saskatchewan and swings north-west to a point on the Saskatchewan-Alberta boundary just south of Lloydminster, thence westward and southward, making an arc roughly through Red Deer and Calgary, and striking the international boundary just east of Glacier Park where it joins up with the western boundary of the Great Plains in the United States. There is another smaller extension of the semi-arid province in southern British Columbia (513).

The western portion of the semi-arid region in the United States is harder to describe; partly because of the topographic irregularities, and partly because it lies in an intermediate moisture belt between the arid and the sub-humid Pacific and mountain zones. In Thornthwaite's (505) earlier scheme, it includes ranges in P-E index from 16 to 31. Under his revised rational classification of climates (507), the semi-arid province would lie in a moisture index range from -40 to -20. It is interrupted by mountains and high plateaux, whose higher portions extend into sub-humid and humid climates, and it often occurs as a broad or narrow belt between coniferous forests and the desert.

The semi-arid region, as described, would include most of the original grassland (excluding tall grass, the south-eastern coastal prairie, marsh grass, and alpine grassland) and the savanna, woodland, and chaparral of various writers (4, 37, 115, 137, 151, 159, 218, 298, 328, 350, 374, 433, 442, 458, 513, 517, 542, 586).

As in the case with the boundary between the semi-arid and sub-humid regions, the boundary between arid and semi-arid is not sharply defined. The severe climatic conditions in the arid centres gradually decrease in severity and finally reach a point where they are considered to be semi-arid. Placing a line of demarcation becomes a matter of drawing a line connecting points having the same degree of aridity in the transition zone between arid and semi-arid. Locating the boundary is made more difficult because of local rainfall conditions, slope exposure, or character of soil.

Shreve (470) outlined the Great American Desert, which is essentially the arid region, as follows:

> ... Beginning at the north it will be seen that desert extends southward from central and eastern Oregon, embracing nearly all of Nevada and Utah except the higher mountains, into south-western Wyoming and western Colorado, reaching westward into California to the eastern base of the Sierra Nevada, San Bernardino and Cuyamaca mountains. From southern Utah the desert extends into north-eastern Arizona at the same time that it occupies the western and south-western parts of that State ......
>
> On the highlands of south-eastern Arizona and southern New Mexico the continuity of the desert is broken by Desert Grassland Transition. At a slightly lower elevation it reappears in the valleys of the Rio Grande and Pecos rivers, extending as far east in Texas as the lower course of Devil's River .....
>
> In the north an isolated area of desert occupies part of the Columbia River basin in eastern Washington ...

Most plant geographers agree in general with the location of the boundary of the desert region in the United States as outlined by Shreve. The map of Schimper (425) was generalized, but it delineated the desert fairly well. Harshberger's (218) delineation agrees reasonably well with the maps of Shreve (458) and Shantz and Zon (442), and there is good agreement between the last two except that Shantz and Zon extend the northern desert further to the east and north west and the "creosote bush" desert farther southward in the Rio Grande plains and adjacent Mexico.

Climate of the arid and semi-arid areas

The general features of the climate of the arid and semi-arid areas have been covered by many investigators (1, 66, 124, 261, 294, 314, 380, 404, 415, 506, 548, 549, 550, 551). A general review of these climatic studies has been made by Meigs (314), and only the more pertinent contributions to the ecology of the areas will be mentioned here.

The Köppen classification of climates as applied to North America by Connor (124) and Ward (551) delineates the arid climates on the basis of drainage patterns peculiar to arid regions. Köppen's findings were reduced to a formula that expresses the mean annual depth of precipitation in centimetres at various mean annual temperatures along the moister limits of the dry climates. These dry climates are designated "steppe" or "desert", depending on whether they receive more or less than half the critical precipitation. Ackerman (1), Ward (548, 550), and MacDougal (294) have discussed Köppen's classification as it applies to the arid and semi-arid areas and have suggested modifications to meet specific conditions in North America. Russell (403, 404, 405) enlarged on Köppen's system by bringing in the frequency of "dry" and "desert" years.

Thornthwaite (505, 507) developed an entirely new system based first on precipitation and evaporation (505) and later on potential evapo-transpiration (507). Jones (250) reviewed the schemes that have been proposed and pointed out the weaknesses in these various systems. Borchert (66) published a study of the climate of North American grassland which consolidated previous information and added further light on the climate of the semi-arid area.

The classification proposed by Meigs (314) appears to be the most useful of the schemes so far developed. It makes use of both the systems built around "temperature" relations and "moisture" relations which are consolidated into a simple and usable system that can be portrayed on maps with a minimum number of symbols to be assimilated by the reader. As far as the semi-arid and arid portions of North America are concerned, the climates as portrayed by Meigs fit very well with the location and extent of the major plant communities. According to Meigs, the climate of the arid and semi-arid portions of the United States varies from hot and extreme arid to cool and dry. Mean monthly temperatures of the warmest month range from about 10°C to more than 30° C., while the mean temperature of the coolest month ranges from below 0° C. up to nearly 20°C. Precipitation varies from almost nothing (471) to 20 inches in Canada and to 25 inches or more in the high evaporation regions of the South West. The evapo-transpiration index varies from -57.7 (314) to the upper limit of -20 as set by Thornthwaite (507).

Prior to 1890, the general classification for floral and faunal areas in the United States was based on a general breakdown into "Eastern", "Central", and "Western", the last extending from the eastern edge of the Plains westward to the Sierra Nevada and including the Rocky Mountains and the Great Basin. At this time, the Department of Agriculture initiated a series of surveys of the vegetation, animal life, and crop zones under the leadership of Dr. C. H. Merriam. In 1890 a new scheme of classification began to evolve under Merriam's (317, 319) guidance. The beginnings of "Merriam's Life Zones" were worked out on the San Francisco Peaks and adjacent area in Arizona (317). Merriam set the northern (or upper) limit of his life zones on the basis of the summation of the daily mean temperatures above 43° F., and the southern (or lower) limit on the normal mean temperature of the hottest six consecutive weeks. The system reached its full development in the publication of Life Zones and Crop Zones of the United States in 1898. In this publication, Merriam (322) separates the arid from the humid exactly along the 100th meridian between latitudes of 35° and 45°. Most of the area we have termed semi-arid and the cooler arid area were included in his "Transition" and "Upper Sonoran" zones, while the hot dry deserts were placed in the "Lower Sonoran" zone. Many of the Western States were surveyed by various workers using the scheme developed by Merriam. Merriam (318) covered the Snake River plains of Idaho which he considered to be characteristically Upper Sonoran. Bailey (23, 24, 25) followed with surveys of Texas, New Mexico, and North Dakota, and Cary (101, 102) reported on the life zones of Colorado and Wyoming. All of these surveys had vegetation maps which are still of value whether or not Merriam's classification is followed.

Merriam's (322) life zones were widely accepted, especially by zoologists, although from the beginning there were a few doubters like Cockerell (118, 119, 120). Hall and Grinnell (201) defended Merriam's classification with some modification, but Shelford (445), Kendeigh (259), and Daubenmire (146) have questioned the validity of Merriam's temperature

summations as related to the distribution of plants and animals. Since the publication in 1921 of The distribution of vegetation in the United States as related to climatic conditions by Livingston and Shreve (280), it has been generally accepted that an adequate classification of vegetal areas based on physical factors needs to recognize moisture relations in one way or another.

Major physiographic features

The most complete discussion of the physiography of the arid and semi-arid portions of the United States is that of Fenneman (175). The semi-arid region east of the Rocky Mountains is roughly equivalent to the Great Plains with southern and south-western extensions into Texas and New Mexico. The eastern boundary is not well defined, but according to Fenneman, there is a definite physiographic break between the Lowlands and the Great Plains. It is marked by a gently sloping ridge 300 to 400 feet high. The escarpment is distinct for hundreds of miles in southern Canada along the Saskatchewan River. As far south as central Kansas there is a mild contrast between the Central Lowland and the higher, more sharply dissected Plains. This same line from the Dakotas to northern Kansas marks the western edge of the glacial drift. In southern Kansas and continuing westward and southward through Oklahoma and Texas, the boundary is marked by a ruggedly dissected escarpment. This eastern line falls close to the 1,500 foot contour line throughout most of its length.

Shantz (433) placed the eastern boundary of the Great Plains region between the 97th and 99th degree of west longitude and mostly east of the 98th degree. The line cuts close to the eastern boundaries of the Dakotas, hits the south boundary of Nebraska about one-third of the way from the south-east corner. The western two-thirds of Kansas and the western half of Oklahoma lie in the Great Plains. The boundary line bends slightly west and then south east in Texas to reach the Gulf Coast at about the 97th degree west longitude. The western boundary averages 5,500 feet in elevation with a range of 1,000 feet above and below that altitude.

In Canada, the chief area of semi-arid territory is a northern extension of the Great Plains and includes about the same elevations except that the western boundary is nearer 4,000 feet.

The Basin and Range and the Great Basin physiographic provinces include most of the arid as well as some of the semi-arid areas in the United States. The region west and south of the Colorado Plateau, embracing one-tenth of the United States and extending into Mexico, is aptly styled the Basin and Range province. Topographically, it is distinguished by isolated, roughly parallel mountain ranges separated by almost level desert basins. Climatically, it is characterized by want of sufficient run-off to reach the sea or to forward its load of detritus.

The Great Basin is really made up of many basins. According to Burr (87), it has a north and south length of 880 miles and an east and west extent of 572 miles. Altogether it includes an area of 210,000 square miles. It is broken by mountain chains typically 50 to 75 miles long and 6 to 15 miles wide.

Soils of the arid and semi-arid areas

On the basis of soils, Marbut (307) set the eastern boundary of the Great Plains along the eastern boundary of the zone of carbonate accumulation. He placed the western boundary along the east side of the Rocky Mountains and fixed the line where mountains do not exist on the basis of soil colour - it is the line between dark-coloured and light-coloured soils. Marbut considered the easternmost or black belt of the Plains area to be the equivalent of the Black Earth or Chernozem of the Steppes in European and Asiatic Russia. The soil is black with the carbonate zone 2 to 6 feet below the surface. The western boundary of this black belt lies approximately along the line between the semi-arid and sub-humid provinces of most climatologists.

Kellogg (256) drew the line between the Chestnut and Chernozem soils slightly east of Thornthwaite's (505) eastern boundary of the semi-arid in the portion of the United States north of Kansas but showed it further west from Kansas south. The climate of the Chernozem zonal group of soils was given as "temperate to cool, sub-humid" and the Chestnut group "temperate to cool, arid". He did not recognize "semi-arid".

In Soils and Men (527), a more detailed breakdown of the soils of the semi-arid and arid areas of the United States is given, and in an article under the authorship of Baldwin *et al.*(27), the breakdown of the major soils groups is shown as follows:

Zonal Soils	Native Vegetation	Climate
Desert	Scattered shrubby desert plants	Temperate to cool; arid
Red Desert	Desert plants, mostly shrubs	Warm temperate to hot; arid
Sierozem	Desert plants, scattered short grass, and scattered brush	Temperate to cool; arid
Brown	Short grass and bunch grass prairie	Temperate to cool; arid to semi-arid
Reddish Brown	Tall bunch grass and shrub growth	Temperate to hot; arid to semi-arid
Chestnut	Mixed tall and short grass prairie	Temperate to cool; semi-arid
Reddish Chestnut	Mixed grasses and shrubs	Warm temperate to hot; semi-arid
Chernozem	Tall and mixed grass prairie	Temperate to cool; sub-humid

In the Canadian portion of the central grassland, Clarke et al. (107) divided the soils into Brown, Dark Brown, and Black, equivalent to the Brown, Chestnut, and Chernozem soils in the United States. Their breakdown is as follows:

Zonal Soils	Native Vegetation	Climate
Brown soils	Short grass to mixed prairie - carbonate layer 6 to 14 inches	Cool; semi-arid
Dark Brown soils	Mixed prairie and submontane	Cool; semi-arid to sub-humid
Black soils	Mixed prairie and tall grass - carbonate layer 18 to 30 inches	Sub-humid

Also in Canada, Mitchell and Moss (326) correlated short grass with Brown, mixed prairie with Dark Brown, and the park belt with Chernozem soils.

MAJOR PLANT COMMUNITIES OF THE SEMI-ARID AREAS

For convenience of discussion, the overall semi-arid and arid areas of the United States and Canada are divided into two major divisions: (1) semi-arid and (2) arid. The semi-arid is again broken into two broad divisions: (a) grassland and (b) woodland and chaparral.

Semi-arid Grasslands

Shantz and Zon (442) divided the grasslands of the United States into seven general types:

Tall grass, or prairie grassland.
Bunch grass, or Pacific grassland.
Short grass, or plains grassland.
Mesquite grass, or desert grassland.
Mesquite and desert grass, or desert savanna.
Marsh grass, or marsh grassland.
Alpine meadow, or alpine grassland.

Of these the short grass, mesquite grass, mesquite and desert grass, and the bunch grass are found in the semi-arid areas.

The short grass lies mostly west of the 100th meridian, the mesquite grass lies south of the short grass and occupies much of the higher land of western Texas and the lower parts of New Mexico and Arizona, and the mesquite and desert grass savanna extends across Texas from the Red River southward

to the Gulf of Mexico. Bunch grass occurs on the plateaux and foothills of eastern Washington and Oregon and western Idaho; also in the foothills and mountain valleys of California and Utah.

Weaver and Clements (566) divided the "grassland climax" (Stipa-Bouteloua formation) as follows:

1. True prairie: Stipa-Sporobolus association
    a. Sub-climax prairie: Andropogon associes
2. Coastal prairie: Stipa-Andropogon association
3. Mixed prairie: Stipa-Bouteloua association
    a. Short grass plains: Bulbilis-Bouteloua associes
4. Desert plains: Aristida-Bouteloua association
5. Pacific prairie: Stipa-Poa association
6. Palouse prairie: Agropyron-Festuca association

Of these the mixed prairie, short grass sub-climax, and the desert plains would definitely fall in the semi-arid category and the Pacific prairie and Palouse prairie at least in major part. Clements and Shelford (115) followed the same breakdown except that Pacific prairie is called California prairie.

The Plains Grassland

The grassland types of both Shantz and Zon (442) and Weaver and Clements (566) extend into Canada. According to Coupland (137), the grassland in Canada extends from the foothills of the Rockies east along the international boundary 750 miles to a point just east of the Red River in Manitoba and north about 275 miles along the Saskatchewan-Alberta boundary. The major grassland area is thus triangular in shape, with the international boundary as the base and with the apex on the Saskatchewan-Alberta boundary. Of this grassland area, the portion between the foothills and the vicinity of the Saskatchewan-Alberta boundary is called mixed prairie by Coupland. True prairie lies to the east and mountain prairie,or fescue grassland, lies to the west. Hubbard (235) recognized three grassland formations in the Great Plains area of Canada, namely, short grass, mid grass, and tall grass.

Tisdale (513) has described an additional grassland area in British Columbia. He showed three zones: Agropyron-Artemisia, Agropyron-Poa, and Agropyron-Festuca, or lower, middle, and upper grasslands. He noted a strong resemblance to the vegetation further south in eastern Washington and Oregon, Idaho,and northern Utah.

The great central grassland in the United States has been treated differently by various writers. There is little difference of opinion regarding the true prairie or tall-grass area, but there is considerable difference as to whether the semi-arid portion should be considered as a mixed grass climax, a short-grass climax, or both.

In his comprehensive treatment of the grassland biome, Carpenter (98) considered mixed-grass prairie as having association rank. He thought that it possessed certain characteristics peculiar to itself, although, in

a broad sense, it is an ecotone between the tall grass prairies to the east and the short grass plains on the west. He agreed essentially with Aikman (4) in setting up individual climaxes for the mixed grass and short grass. This opinion is not shared by Clements (112), Weaver and Clements (566), and Clements and Shelford (115) who did not recognize the short grass as climax, nor by Shantz and Zon (442) who did not recognize a mixed grass climax.

In 1897 Clements (110) stated that the two principal formations of the high plains of western Nebraska were the Stipa comata formation and the pepper-grass cactus formation. A year later, Pound and Clements (373, 374) divided the "Prairie Province" into the prairie region, the sand hill region, and the foothill region. They stated that "Prairie formations are of two types, the prairie grass and the buffalo grass formation". They described the buffalo grass formation as including two types: the Bulbilis type and the Bouteloua type. In his earlier publications, Clements (111, 112) considered the short grass to be climax in the Great Plains, but later (113) he considered it to be a disclimax due largely to grazing. Weaver and Clements (566) and Clements and Shelford (115) reiterated the same viewpoint.

The mixed prairie of Clements (112), which included a large portion of the semi-arid climatic region, extended from central North Dakota and South Dakota, central Nebraska, and north-western Kansas throughout Montana and Wyoming to the Rocky Mountains and southward in Colorado along the foothills of the front range. It also extended into Saskatchewan and Alberta. The mixed prairie of Weaver and Clements (566) and Clements and Shelford (115) is more extensive - from northern Alberta and Saskatchewan through the Staked Plains of Texas and from central North Dakota and Oklahoma on the east to western Wyoming and eastern Utah and south westward through northern New Mexico and Arizona to the Colorado Valley.

Shantz (433) divided the great grassland area which extends from the forests of the East to the foothills of the Rocky Mountains into the tall grass formation or prairie grassland and the short grass formation or plains grassland.

> The prairie is a relatively tall wheat-grass or bluestem grassland, while the plain is a short buffalo and grama-grass or grama-grass land. In general appearance the vegetation of the plains resembles a closely pastured field, while that of the prairie resembles a relatively luxuriant meadow.

According to Shantz (433), the boundary between these formations is not topographic. It lies along the 2,000 foot contour with the country to east and west topographically similar. On the basis of soils, the dividing line is sharper but the change is gradual. The division line corresponds to the rather sharp line that marks the western edge of the Chernozem zone. Where carbonate accumulation occurs above 2 feet, the plains type predominates; where deeper than 30 inches or entirely lacking, the prairie type of grassland occurs. Short grass characterizes areas where each season all available soil moisture is consumed by plant growth.

Carpenter (98) limited mixed grass prairie plains to a strip running from central Saskatchewan, north-western and south central North Dakota, through central South Dakota, Nebraska (exclusive of the sand hills), Kansas, and the western part of Oklahoma to northern Texas.

Schaffner (423) considered the grass association occurring in a belt approximately one hundred miles wide and occupying most of the Chernozem soils as mixed grass prairie plains. He listed the dominant grasses as Andropogon furcatus and Andropogon scoparius, together with the short grass dominants from the west - Bouteloua gracilis, Bouteloua hirsuta, and Buchloe dactyloides. Schaffner recognized a dovetailing of grass associations of high and low topographical levels resulting in an irregular boundary belt rather than a sharp line. He also found that the western limit of the true prairie in middle latitudes coincided with the eastern limit of the prairie dog and the harvester ant, and that the Pedocal-Pedalfer division line of Marbut (307) fell within the same zone.

Taylor and Loftfield (498) have shown that the Zuni prairie dogs may destroy 100 per cent of the forage grasses and that they have the same preferences as cattle, hence, it is quite likely that prairie dogs did exert a strong influence in the vegetation of the Plains.

Larson (271) insisted that the term "disclimax" should not be applied to the short grass association, as any over grazing in recent years was matched by buffalo in pristine times. As the short grass vegetation developed under grazing by bison and other animals which were normal to the biome, it is not correct to call it "disclimax". Probably the strongest evidence indicating the antiquity of the short grass and its climax character is to be found in the soil. It would be practically, if not entirely, impossible for a shallow carbonate layer to have developed under a dominant cover of mid or tall grasses. Also, the lighter colour of the soils under the plains short grass is evidence of a different combination of climate, vegetation, and soil than is to be found in the area where taller grasses are dominant. As Bruner (82) has pointed out, the dense cover of short grasses together with compacted soils in a region of low rainfall results in the formation of hardpan, and these conditions together will maintain the dominance of the short grasses.

Aikman (4) suggested a modified version of the mixed grass transition. He fixed the eastern boundary of the mixed prairie as a line west of which prairie grasses, because of a shortage of water, no longer entirely dominate the area but share dominance with short grasses. According to Aikman,

> The western boundary of the mixed prairie may be described as a line east of which sufficient rain falls and penetrates the soil to wet it periodically to a depth varying from 24 to 30 inches. Plants whose roots penetrate the soil to a depth of 24 inches or more obtain moisture for sustained growth for a period of at least 2 1/2 months each year even in drought years. The presence of a permanent tall grass population is thus ensured.

To the west of the area just described lie the vast plains of the short grass country. The adaptation of the short grasses to the heavy soils and light precipitation of this region (and to similar soils in the mixed prairie region) is quite definite. In the heavy, fine textured soils, percolation of moisture is slow and limited in depth, and there is a high percentage of run-off, especially of the heavier rains, so that for months of the year the subsoil may remain dry. The short grasses make the fullest use of the topsoil moisture. Their root systems, fibrous and shallow, almost completely cover the area, taking up the small amount of available water in a limited time, and their season's growth and reproductive processes are completed in a few weeks.

Because of the complete occupation of the top few inches of the soil by the fine, fibrous roots of the blue grama and buffalo grass, these grasses are shown to be the true dominants of the community.

Hayes (220) made the following statement regarding the tall grass-short grass transition: ". . . Tall grasses are dominant only in valleys and on sandy soils, generally giving way westward to short grasses through the relatively narrow transitional zone of mixed prairie."

The plains grassland, short grass or mixed prairie or both, has been the subject of a great deal of study from north to south and east to west, and there is general agreement on the broader aspects of the floristic composition and ecological structure -- and in general, on successional relationships -- although there are differences in terminology.

Two outstanding and well-documented reviews of the ecology of grassland have been published by Hanson (205, 207). These are basic reference works that provide a wealth of material on the fundamental aspects of the ecology, floristics, and structure of the plant communities that make up the North American grassland. To these might well be added Malin's (302) publication _The Grassland of North America_, a rather comprehensive and refreshing treatment with an excellent bibliography; the United States Department of Agriculture Yearbook for 1948 entitled _Grass_ (529); and Carpenter's (98) The _Grassland Biome_.

Many other excellent articles cover specific phases or specific areas of grassland, and a considerable number of these relate to composition of the plant communities and the distribution of the more common grasses. Clarke (106) listed _Bouteloua gracilis_, _Stipa comata_, and _Koeleria gracilis_ as dominant grasses in Saskatchewan and Alberta. Clarke _et al._ (107) divided the western portion of the central grassland into three associations:

Short grass prairie: _Bouteloua-Stipa_ association
Mixed prairie: _Stipa-Agropyron-Bouteloua_ association
Submontane mixed prairie: _Festuca-Danthonia_ association

The grassland gives way to parkland (aspen and willow) on the north. In the short grass prairie, blue grama makes up from one-fourth to two-thirds of the basal grass cover. Stipa comata, Agropyron smithii, Keoleria cristata, blue grasses, other grasses, sedges, forbs, and shrubs make up the remainder. The same plants are present in the mixed prairie but in a different proportion, and more mid and tall grasses are present. Sarvis (416) considered Bouteloua gracilis and Stipa comata as dominants in North Dakota. Hanson and Whitman (211) added Agropyron smithii. Whitman et al. (591) recognized tall grass, mixed prairie, and short grass. Craig (140) pointed out that the principal characteristics of North Dakota are flatness, aridity, and severe winters. Stevens (481) listed plants for North Dakota according to Merriam's life zones. Hayward (222) recorded mixed prairie vegetation skirting the Black Hills of South Dakota. Morris (327) classified plants of the grassland (and adjacent areas) in Montana by moisture and temperature requirements, soil, grazing resistance, and other factors. Wright and Wright (597) divided the Montana grassland into five types based on a study of ten relict communities. As early as 1887, Bessey (41, 42) divided Nebraska into districts and described the vegetation -- particularly the woody species. Hopkins (232) described four principal plant communities native to the loess hills of Nebraska. Bouteloua is the most abundant grass in the mixed grass community and also is the most drought resistant. Less moisture was present in the soil where Agropyron smithii -- a grass which becomes of much greater importance southward -- was the dominant in the community.

Visher (541, 542, 543) described the buffalo-grama grass or climax steppe association in the Great Plains extending to the east on well-drained clay soil and to the west under conditions where run-off is less rapid. He also noted various modifications of steppe vegetation as related to differences in topography, exposure, and soils. Aldous (14) showed similar topographic relations in Kansas but classed the western three-fourths of the State as mostly short grass.

Albertson (5) has described in detail the ecology of the mixed prairie near Hays, Kansas. He noted that Bulbilis dactyloides and Bouteloua gracilis in almost equal mixture occurred on the nearly level uplands and on impervious clays of the lower slopes. Bunch grass type, dominated by Andropogon scoparius, covered the thin soils of the slopes, while the moist lowlands were characterized by tall and mid grasses including Andropogon furcatus, Bouteloua curtipendula, Agropyron smithii, and Sporobolus drummondii.

On the basis of extensive range surveys, Costello (132) stated that blue grama was the most common grass in both the Colorado and Wyoming plains section. Buffalo grass was second in Colorado but was not important in Wyoming. Agropyron smithii was important in both States. Dodds et al. (161), Shantz (430), and Vestal (538, 539) found blue grama to be the dominant grass in the plains grassland adjacent to the foothills in Colorado. The taller grasses were locally dominant on the steeper slopes, on the more open soils, and in bottoms receiving run-off from the slopes. Livingston (282) found true prairie species on soils from granitic materials in the Black Forest and was of the opinion that they were relict of a former climax. Rogers (393) found the vegetation on immature soils from basaltic rocks in southeastern Colorado varied from short grass to ponderosa pine.

In Oklahoma, Blair and Hubbell (52) divided the State into three major areas on the basis of floristic affinities: eastern deciduous forest, Great Plains grassland, and southern Rocky Mountain. Bruner (82) noted that the short grass association was characterized by the complete dominance of short grasses and by the absence of tall grasses. The transition to desert grassland begins along the Oklahoma-Texas line.

In 1888 Nealley (338) described the grasslands of Texas, and 15 to 20 years later, Bray (71, 72, 73) showed the Edwards Plateau as marking the southern end of the Great Plains. He recognized semi-humid black soil prairies with rainfall of 30 to 35 inches, semi-arid middle plains between the 98th and 101st meridians, and the arid high plains with a rainfall of less than 20 inches. The last merges into the sotol country and the Chihuahuan Desert. Tharp (500) has indicated the significant features of the mesa region and has pointed out the influence of edaphic factors in the distribution of vegetation. Blair (51) and Webb (574) have suggested the division of Texas into biotic provinces or regions. Tharp (501) has recently published an excellent discussion of Texas range grasses by regions based on physiography, soils, precipitation, and evaporation.

The importance of buffalo grass in the Great Plains has been brought out by Wenger (578) and by Beetle (34) who supported his observations with 177 citations. Both men mentioned its wide adaptability to nearly all soils except sands and its maximum development on heavier soils. It is alkali-tolerant and will grow on poor or eroded soils. Webb (573) called attention to the rapid growth of both roots and stolons. Roots of one plant reached a depth of four feet eight inches in one season, and another plant produced 650 feet of stolons at the age of 84 days. Porterfield (372) pointed out the resistance of buffalo grass to submersion -- it survived under as much as 59 inches of water over a period of 19 months.

Within the Plains area, the most significant physiographic feature so far as vegetation is concerned is the presence of extensive sand hills in Nebraska and smaller sandy areas in other States, particularly Kansas and Colorado. In the western Nebraska sand hills where precipitation averages about 18 inches, Tolstead (516) observed that there was a wide variety of habitats caused by differences in soil textures, drainage, and topography. There was no run-off from sand, and loss from evaporation from the surface was small. Fine sandy loams were less efficient in absorption of rain. High temperatures, low humidity, prevailing south winds, and frequent droughts were unfavourable to plant growth. He noted that mesophytic tall grass communities were found in sub-irrigated meadows, tall grasses and bunch grasses dominated sands, mixed prairie grasses occurred on fine sandy loams, and buffalo grass was found only on overgrazed hard lands. Ramaley (378) found that the same tall grasses were dominant in the sand hills of Colorado under a rainfall of 10 to 15 inches. Where the sand hills became well stabilized, blue grama and buffalo grass became dominants. Doell (162) considered the flora of the sand hills of Kansas represented a transition between tall and short grass prairies.

Desert grassland and mesquite and desert grass savanna

The boundaries of these southwestern grassland types and the distinction between them are not treated alike by all writers. Shantz and Zon (442) considered them to be separate types. According to them,

> The Desert Grassland reaches its best development in southeastern Arizona, southern New Mexico, and western Texas. Wherever curly mesquite is predominant, this type in many respects resembles the Shortgrass Type of the Great Plains. Temperatures are such that growth is likely to occur whenever rain falls. However, because of the seasonal distribution of rainfall, the principal growing season is in July and August. Precipitation is generally greater than 12 inches per year except in southern New Mexico where the yearly average is generally somewhat below 12 inches.

The mesquite and desert grass savanna is similar to the desert grassland but has a higher rainfall and a deeper layer of periodically moistened soil.

The desert plains association of Weaver and Clements (566), in addition to covering about the same area as Shantz and Zon's desert grassland, extends to the 5-inch isohyet, whereas the latter considered 12 inches of precipitation to be the minimum for grassland in most places. Clements (114, 115) contended that much of what is now desert shrub was once grassland before overgrazing destroyed the grass. Whitfield and Beutner (586) also separated the desert plains grassland from "desert scrub" along the 5-inch precipitation line.

Carpenter (98), although recognizing its partial grassland character, eliminated the mesquite-desert grass savanna from the grassland biome. He considered it to be an area of ecotone to the desert types of the Rio Grande region. On the basis of changes in a protected desert grassland area, Brown (81) concluded that desert grassland was not climax but was maintained in part by some factor that was unfavourable to shrubs. Humphrey (240, 241) considered that fire might be the controlling factor, at least for the smaller shrubs. Canfield (96) found that once unpalatable shrubs and trees are established, they become a relatively permanent part of the plant cover.

Pacific prairie and Palouse prairie or Pacific grassland

According to Weaver and Clements (566), the Pacific prairie of California consists of mid grasses and hence has the same general appearance as the mixed prairie; however, it has been so largely destroyed by overgrazing and fire that it is difficult to find typical remnants. Munz and Keck (335, 336) divided California grasslands into two communities: coastal prairie and valley grassland. Sampson et al. (413) stated that nearly all of the Central Valley was formerly grassland, but only a narrow fringe bordering the woodland grass formation of the foothills was left. Piemeisel and Lawson (368)

described the various types and changes in vegetation in the San Joaquin Valley as related to climatic conditions and pointed out the successional changes.

The Palouse prairie of Weaver and Clements (566) resembles the mixed grass prairie and has many dominants in common with it; it also has common floristic relationships with the Pacific prairie and like it depends upon winter rainfall. It is characteristic of eastern Washington and Oregon, southern Idaho, and northern Utah. They noted this grassland has been largely replaced by sagebrush and annual grass communities. Stoddart (485) has shown the close relationship of vegetation in the valleys of northern Utah to the prairie farther north and west, and Myers (337) mentioned that sagebrush has extended its range in Idaho. Many others (138, 148, 154, 330, 364, 365, 366, 367) have called attention to the changes that have taken place in this grassland since the arrival of the white man.

Shantz and Zon (442) included the Pacific prairie and the Palouse prairie in their Pacific grassland which they divided into: wheat-grass sod, wheat-grass bunch, and Stipa-Poa-bunch grass, the last in the Central Valley of California. They concluded that the reason there are no short grasses in the Pacific area is because of the lack of summer rains under which short grasses thrive.

Woodland

The woodland formation as described by Weaver and Clements (566) consists typically of small trees 20 to 40 feet high belonging to the three genera Juniperus, Pinus and Quercus. They are all evergreen xerophytes and more or less subtropical in their temperature relations. The woodland is essentially a southwestern xeric formation, mostly below altitudes of 7,000 feet. It finds its best expression on the high plateaux of the Colorado Basin but occurs from the Edwards Plateau and the Davis and Guadalupe Mountains of western Texas through northern Mexico to Lower California (71, 341, 357). It extends northward along the foothills in New Mexico and Colorado to southwestern Wyoming and thence westward through Utah and Nevada to northern California (155, 275, 442). At its lower limit, it meets grassland, sagebrush and chaparral and at its upper limit, it gives way to the yellow pine consociation.

According to Daubenmire (150), the pinon-juniper type covers 76 million acres in the United States extending from Mexico northward to the Snake River in Idaho and along the east slope of the Rockies to Colorado Springs, Colorado. He noted that when stands were overgrazed, the trees or shrubs increased. In the southwestern United States, the pinon-juniper may alternate with an oak mountain mahogany brush type. Foster et al. (180) have observed that the Edwards Plateau, the eastern limit for Rocky Mountain timber species, is the meeting place for Atlantic and Mexican species as well. In the studies of the Stockton Plateau a little farther west and in the more arid portion of Texas, Webster (575) noted that Juniperus Ashei alternated with Larrea and Flourensia and thought this area might belong to the desert rather than to woodland.

Woodbury (594) studied the distribution of the pinon-juniper woodland in Utah. He used the term "pigmy conifers" in describing what he called the "pigmy forest". He explained its distribution on the basis of climate and the interaction of all factors affecting moisture. He noted particularly that sagebrush occupied the fine soils and conifers the coarse gravelly or rocky soils.

Emerson (170) found that differences in precipitation did not account for distribution of pinon-juniper in northeastern New Mexico. It occurred on a variety of soils but most often on rocky ledges. He also noted that in the successional development, juniper was the pioneer followed by pinon. Pearson (357) noted that distribution of pinon-juniper in northeastern Arizona is determined by a compromise between favourable moisture and temperature conditions.

Chaparral

According to Cooper (128), the centre of distribution of the broad sclerophyll vegetation is in southern California west of the deserts. The area of 10 to 30 inches of rainfall is the region of broad sclerophyll dominance -- above 30 inches, conifers become prominent, and below 10 inches begins the transition to deserts. Two main communities were recognized by Cooper: broad sclerophyll forest formation and the chaparral formation. He divided the latter into two associations: (1) the climax chaparral association which is the dominant community over the southern coast range and the mountains of southern California and northern Lower California; Adenostoma fasciculatum is the most common species, while the genus Arctostaphylos gives its stamp in certain localities; (2) the conifer forest chaparral association which is nearly coextensive with the montane conifer forest in northern California and Oregon. This association belongs to the sub-humid region.

Plummer (370) distinguished between true chaparral, a sclerophyllous woodland or mixed forest of stunted trees related to peculiar climatic conditions in California and "mock" chaparral in Arizona, New Mexico, Colorado and Utah. He considered true chaparral to be climax, while in other areas the shrubby growth would be replaced by forest. This same is true in parts of California.

The chaparral climax of Clements (112, 113) and Weaver and Clements (566) included a greater range of physical conditions and vegetation than the chaparral of Cooper (128) and Plummer (370). The Clements' concept recognized a Quercus-Ceanothus formation which was divided into:

1. Petran chaparral: Cercocarpus-Quercus association
   (a) Oak-sumac sub-climax: Quercus-Rhus associes

2. Coastal chaparral: Adenostoma-Ceanothus association

The latter is essentially the chaparral of Cooper and Plummer.

As described by Weaver and Clements (566), the chaparral formation is characterized by shrubs of the same general life form. It is more xeric than forest but less so than sagebrush and "desert scrub" which it resembles in physiognomy. Climatically, it is intermediate between grassland and forest and is best developed in sub-tropical regions that incline toward desert. Shantz and Zon (442) were largely in agreement with Weaver and Clements in their treatment of chaparral.

Chaparral reaches its typical development on the foothills of the southern Rocky Mountains, the interior ranges in Utah and Arizona, and on those of the Sierra Nevada and Cascade Mountains and coast ranges of the Pacific slope (442, 566). According to Hayward (221), it possesses many of the characteristics of an ecotone in Utah, and Baker and Korstian (26) found it extending to altitudes where ponderosa pine would be expected to occur. They explained the absence of pine in this case on the basis of insufficient moisture during the summer. In reduced form, chaparral extends northwestward from the Black Hills to the Blue Mountains, and, as a narrow sub-climax band, it borders much of the western edge of the deciduous forest. Somewhat similar sub-climaxes of dwarf oaks, called "shinnery", are found on sandy soils in the southern portions of the mixed prairie.

The coastal chaparral which is the type of vegetation some writers refer to when they use the term "chaparral" has its centre in southern California (172) and extends into southern Oregon, the lower slopes of the Sierra Nevada, southeastern California, and into Lower California. Some authorities extend its range into Nevada and Arizona (442, 341). The major dominants are *Adenostoma fasciculatum*, several species of *Ceanothus*, *Arctostaphylos pungens*, *A. tomentosa*, *Quercus dumosa*, *Prunus ilicifolia*, and *Rhamnus crocea*.

The "California" chaparral has been the object of a considerable amount of investigation. Bauer (31, 32) conducted detailed studies on the composition and factors affecting distribution of chaparral. De Forest and Miller (156) studied environmental conditions of chaparral in the outskirts of Los Angeles. Pequegnat (362) made a similar study including the biota of the Santa Ana Mountains. Miller (324) measured physical factors and growth at elevations from 1,500 to 5,000 feet on north and south slopes near Glendora, California. He noted that 75 per cent of the 21 to 41 inches of rainfall fell from December through March and considered the amount of soil moisture was the most important factor in bringing about the differences in plant cover. Shapiro and De Forest (443) found that soil water available to the plant may be the most influential factor in its rate of transpirational water loss. They also noted that structural arrangement of the leaf or its covering furnished little reliable information on the use of water. Whitfield (585) found that the water loss in coastal sagebrush and coastal chaparral near Santa Barbara, California, were approximately the same. He recorded the highest osmotic concentrations in chaparral in February and April.

Kittredge (262, 263) made studies of the "forest floor" under chaparral and observed that the amount, volume and weight of the materials of the floor played an important rôle in the moisture régime. He found the

annual accumulation of organic material varied from 0.2 to 1.4 metric tons per acre with a general average of 0.6 metric tons.

Additional papers on chaparral are reviewed under the subject "Fire as a factor and as a tool in management".

MAJOR PLANT COMMUNITIES OF THE ARID AREAS

Forrest Shreve (470) who devoted most of his lifetime to the study of the desert vegetation of North America summarized the pertinent available information in 1942. Shreve did not attempt to define "desert" too specifically but stated that the desert has a number of important physical features:

> These include: low and uncertain rainfall, high percentage of sunshine, low atmospheric humidity, high diurnal air temperature, great daily range of temperature, intermittent streams, active erosion by water and wind, high salt content of soil and many minor features related to these.

Shreve included a map showing the North American Desert which he subdivided into: Great Basin Desert, Mojave Desert, Sonoran Desert, and Chihuahuan Desert. He dismissed the idea of separating out a "Colorado Desert" in western California as the area has no features to distinguish it from adjacent areas, and because the name is ambiguous.

Harshberger (218) recognized three subdivisions of the North American desert area, namely, Great Basin region, Sonoran Desert region, and Chihuahuan Desert region. Shantz and Zon (442) divided what they termed "Desert Shrub" into: sagebrush, or northern desert shrub; creosotebush, or southern desert shrub; and greasewood, or salt desert shrub. Clements (112) recognized the sagebrush climax formation which "is essentially a scrub desert" and the desert scrub climax formation which he described as having a rainfall range of 5 to 12 inches, but later (114), he restricted the climax to an area having less than five inches of precipitation. Weaver and Clements (566) gave a rainfall range of 3 to 6 inches for their desert scrub climax. Munz and Keck (335, 336) classed all the desert types of California under "scrub" (a name disliked by many students of desert vegetation) with the following subdivisions: northern coastal scrub, coastal sage scrub, sagebrush scrub, shadscale scrub, creosotebush scrub and alkali sink.

The Great Basin Desert or Northern Desert Shrub

Shantz and Zon (442) divided the northern desert shrub into three main associations and a number of minor communities. The main associations listed were: sagebrush with eight subdivisions, shadscale with three, and salt sage with one. According to Shantz and Zon, the sagebrush type is best developed in the northern and more elevated portion of the area on well-drained soils where precipitation ranges from 10 to 15 inches. The shadscale association is more common toward the south and usually lies below the

sagebrush and above the salt desert shrub. Salt sage ranges farther north than shadscale and occupies large areas in Wyoming, Colorado and Utah. They also recognized a salt desert shrub on poorly drained and saline soils. Shantz (434) divided the northern desert vegetation of Utah and Nevada into nine communities, seven of which were given association rank. The breakdown differed from that of Shantz and Zon in minor ways but was not essentially different considering that all communities of the northern desert were not found in Utah and Nevada.

Billings (45, 46, 48) published a series of articles covering his comprehensive studies of the desert areas of Nevada, California and Utah. In the first paper, he described 15 associations in western Nevada. In the second, he proposed to separate an Atriplex association from the Atriplex-Artemisia association of Clements (112). Billings (46) contended that this association, in a rather pure form, extended from the Carson Desert of west central Nevada south and east to the dry mountain ranges of the Death Valley region. As he described it, this association lies between the creosotebush association on the south and the Artemisia association on the north. It is characterized by the almost universal presence of Atriplex confertifolia. Billings (48) reaffirmed his contention of the validity of an Atriplex association in his review of the vegetational zonation in the Great Basin. He recognized from south to north the following zones: (1) creosotebush (Larrea divaricata), (2) shadscale (Atriplex confertifolia), and (3) sagebrush (Artemisia tridentata) grass.

Other studies included those of Graham (195) who divided the mixed desert shrub of the Uinta Basin into seven associations: (1) Sarcobatus, (2) mat Atriplex, (3) Kochia-Hilaria, (4) Chrysothamnus, (5) Atriplex-Tetradymia, (6) low altitude Artemisia, and (7) Eurotia; Tanner (494) who considered the desert vegetation along with other vegetation in a biotic study in southern Utah; and Fautin (174) who included plants, animals and soils in a comprehensive study of the desert shrub biome in western Utah. He studied sagebrush and shadscale communities in particular and noted that sagebrush grew where moisture was greater and where soils were more permeable and relatively saline free. Shadscale occupied the more xeric areas where the soil was impregnated with mineral salts.

In 1898 Nelson (339) observed that the Red Desert of Wyoming included all that arid section of salt impregnated soil in southern Wyoming in which the salt sages predominated. In 1939 Vass and Lang (536) restudied the Red Desert and found that it had not changed materially in 40 years.

H. P. Hansen (203) studied the post-glacial vegetation of the northern Great Basin and noted evidence of a warm, dry period with a high proportion of grasses and chenopods 4,000 to 10,000 years ago.

The Southern Desert

The southern desert shrub as described by Shantz and Zon (442) includes the following main associations:

Desert saltbush (Altriplex polycarpa)
Creosotebush (Covillea tridentata)

Yucca-cactus
California sagebrush
Mesquite (Prosopis juliflora)

Clements (114) limited what he called "desert scrub climax" to a small area confined to the Death Valley, the Mojave and Colorado River regions, and parts of Mexico. He considered the isohyet of five inches to mark the disappearance of grass dominants and this line was the readiest means of setting off the desert climax.

Weaver and Clements (566) treated what they termed the "desert scrub" (Larrea-franseria formation) as follows:

1. Desert scrub: Larrea-franseria association
   (a) Bronze scrub: Larrea-flourensia associes
   (b) Mesquite: Acacia-prosopis associes
   (c) Sotol: Agave-dasylirion associes
   (d) Thorn scrub: Cereus-fouquiera associes

Shreve (470) preferred geographical, rather than vegetational, designations for subdivisions of the desert because he believed them to be simpler and more generally understood and because plant and animal geographers had used them for a long time. His Mojave, Sonoran and Chihuahuan Deserts combined are roughly equivalent to Shantz and Zon's (442) southern desert shrub but are more inclusive than Weaver and Clements' (566) "desert scrub".

According to Shreve (470), the Mojave Desert is the smallest unit of the North American Desert and lies almost wholly in California. It lies in the southeastern part of the State, east of the southern end of the Sierra Nevada and north and east of the San Bernardino Mountains, extending east to the Colorado River and north approximately to the 4,500-foot contour in California and Nevada. While it includes the famous Death Valley which drops to 480 feet below sea level, nearly three-fourths of its area lies between 2,000 and 4,000 feet. At the higher elevations Yucca brevifolia dominates the landscape and at the lower elevations Larrea divaricata dominates the vegetation.

The Sonoran Desert occupies the lowlands surrounding the upper part of the Gulf of California, the southwestern quarter of Arizona, the lowlands of Baja California, and the western half of Sonora, Mexico. Larrea divaricata and Franseria dumosa dominate the lower portion of the desert, but they are joined by many shrub, tree and succulent sub-dominants which become more and more prominent toward higher elevations and greater rainfall. The Sonoran Desert is noted for the richness and variety of its flora.

The Chihuahuan Desert includes parts of New Mexico and western Texas adjacent to the Rio Grande, the lower valley of the Pecos, and extends into Mexico.

References to the deserts include a wide field covering their physical conditions and their biological and economic relationships. They start

with the scattered notes of the early explorers and culminate with Shreve's (471) monograph on the Sonoran Desert. Only the more representative contributions can be mentioned here, but these, together with the bibliographies included in the various publications, should open the doors to those interested in making more extensive studies of desert ecology.

In 1877 Hoffman (229) published a paper on the vegetation of Nevada and Arizona. In the 1890's, Townsend (520, 521) published two papers on the biogeography of the southwestern United States and adjacent lands in Mexico; Merriam (320, 321) completed companion papers on the shrubs and on the cacti of the Death Valley Expedition, and Bray (70) showed the close relationship between the flora of the Lower Sonoran zone in North America to the flora of the arid zones of Chile and Argentina. A few years later, Bray (72) published an excellent description of the vegetation of the drier portions of Texas. Cockerell (120) compared the vegetation of the Salt River Valley in Arizona to the Mesilla Valley in New Mexico and found much in common except that the Mesilla Valley was cooler. Forty-five years later, Cockerell (121) returned to the desert and prepared a paper entitled Colorado Desert of California -- Its Origin and Biota.

The Desert Laboratory of the Carnegie Institution of Washington, located at Tucson, Arizona, opened in 1903. Early work at the laboratory was chiefly concerned with the physiological and ecological behaviour of some of the characteristic plants of the immediate vicinity and with the conditions to which they were subjected; but a few general studies of the desert were included. D. T. MacDougal (286), the early director of the Desert Laboratory, published a paper on some aspects of desert vegetation the year the laboratory opened. He noted that the mesas adjoining the Gulf of California offered the most extreme desert conditions in North America (287). The precipitation at Yuma, Arizona in 1903 was 25 mm, and at points further south no precipitation occurred. The vegetation consisted of types devoid of massive storage organs. Species with spinose branches and with minute leaves which are quickly discarded during unfavourable periods were abundant. In 1908 MacDougal (288) completed a monograph on the botanical features of North American deserts. In the same year, he (289) published a series of articles in Plant World on the course of vegetative seasons in southern Arizona. In these articles he noted that winter annual seeds have special powers of endurance as they show no activity when soaked by rains and exposed to heat of over 100° F. on the surface of the soil in summer, but in December the seeds germinate. He believed some winter annual seeds needed the warmth and moisture of summer followed by the cool, moist weather of autumn and winter. In some species, germination was induced by simulating summer heat and winter coolness by use of oven and refrigerator. In 1912 he (290) discussed North American deserts in general and noted that in Utah the annual evaporation rate was 50 inches, which was five times the maximum and six times the average rainfall. He also noted the great variation in rainfall; for example, the maximum annual rainfall in the deserts of Utah was two and one-half times the minimum, while near Tucson the maximum might be five times the minimum and in the Chihuahuan Desert nine times the minimum.

On his first trip to the Sonoran Desert, Blumer (62) was impressed with the richness of the desert flora. A similar impression was gained by

Paulsen (355) who was particularly interested in the comparison of life forms according to Raunkiaer's (379) system.

Spalding (478, 479) described the local vegetation in the vicinity of the Desert Laboratory in detail and discussed the factors influencing distribution. He observed that soil properties and aspect were of paramount importance in determining local distribution. Soil water was most important but aeration and alkali were also important. He noted that creosotebush showed high capacity for adjustment and "perfect indifference" to change of aspect.

Forrest Shreve joined the staff of the Desert Laboratory in 1909 and retained his connexion with the institution until 1945 and continued his desert studies until his death, 19 July 1950. During this period, he published over 40 important papers related to deserts.

Several of Shreve's papers dealt with the general aspects of deserts, their vegetation and general characteristics. In summing up his observations on the ecological aspects of the deserts of California, he (463) stressed the dryness of the southeastern part of the California deserts; for example, he recorded four periods in 12 years (1909-1921) in which no measurable rain fell for over 12 months. Eastward in Arizona, annual precipitation was heavier because of the addition of summer rainfall.

On the basis of results obtained from a series of plots on the Desert Laboratory grounds, Shreve (464) reported on changes that had taken place under complete protection between 1906 and 1929. He noted an increase of perennial plants on the level ground, and from 7 per cent loss to 14 per cent gain on the slopes of Tumamoc Hill. In 1937 with Hinckley, he (472) again noted the changes that had taken place over a 30-year period. This study showed that all areas established in 1906 had increased in total plant population from 42 to 851 per cent under 30 years protection from grazing. The increase was greater in the last eight than in the first 22 years. The number of large perennials remained about the same, the increase being due to newly established shrubs and bushes, and to grasses which were negligible in 1906.

In a semi-popular discussion of the problems of the desert, Shreve (467) made the observation that with plants it is relatively easy to detect features of structure which serve to reduce water loss or to provide a reserve of water. But among the mammals of the desert, it is almost wholly the features of behaviour that enable them to live in areas of high temperature and little water. To a greater or lesser degree, the same is true with birds, reptiles and insects. Sumner (490) has likewise noted that desert mammals are not exceptionally well adapted to endure high temperatures. However, burrowing mammals are largely nocturnal, and in the burrows where they spend their days, the day-time temperatures are much lower than those above ground.

Shreve (468) pointed out that, contrary to common opinion, sandy areas are not common in the North American deserts. The prevailing type of surface is stony or hard although there are many small areas of stable,

windblown sand. Only in a few areas along the international boundary and scattered from California to Texas are there sandy areas so extensive that the aspect of the surface affects plant and animal life.

In another paper which summarized the distribution of Larrea as related to environmental factors, Shreve (469) observed:

> For the majority of dominant plants in moist regions there is considerable evidence that they find their optimum conditions near the geometrical centers of their ranges. For desert plants this frequently is not the case. The centers of their areas are usually regions of great aridity, in which they are able to persist but do not reproduce as abundantly, occur in such heavy stands, or grow as rapidly as they do on approaching at least some section of their periphery. This is the case with Acacia paucispina, Carnegiea gigantea, Franseria deltoidea, Fouquieria splendens, and a number of other plants of the Sonoran Desert.

Shreve (470) summarized the available information for the arid areas in a paper entitled The Desert Vegetation of North America. This has become widely recognized as the outstanding reference on the ecology of the deserts of North America; and while Shreve did not agree with many other ecologists on the structural and successional aspects, his straightforward, objective observations serve as a basis for the better understanding of the vegetational relationships of the desert.

For many years, Shreve (471) made comprehensive studies of the Sonoran Desert. The results of his portion of this study were published in 1951, a year after his death. This publication, Vegetation of the Sonoran Desert, embodied the results of studies at the Desert Laboratory and throughout the area of the Sonoran Desert. This and his earlier papers cannot all be adequately summarized in the space available for this review, but pertinent parts have been referred to as they fit into the discussion.

In association with various other workers, Shantz made some notable contributions to the desert literature. Aldous and Shantz (15) listed 16 types of desert vegetation, gave brief descriptions, and indicated the possible economic importance of each. Shantz and Zon's (442) Natural Vegetation in the United States was published the same year as was also a joint paper by Shantz and Piemeisel (440) on the indicator significance of the natural vegetation of the southwestern desert region. The purpose of the latter study was to determine what conditions had led to the development of the principal types of vegetation, and what these types of vegetation signify in terms of the crop-producing capabilities of the land on which they grow. Included were studies of vegetation, climate and soils in the Coachella Valley in California and the Gila Valley of Arizona.

Other general studies include those of Parrish (352) who found that relatively few plants of the Mojave and Colorado Deserts had organs adapted to water storage, the great majority of these plants depending on structures

which restrict evaporation or upon rapid winter growth and dormancy (mostly as seeds) during the long rainless summer. Dice (158) conducted studies over a period of years in an area he termed the "Sonoran biotic province" which agrees fairly well with Shreve's (471) Sonoran Desert. In this paper he discusses both plant and animal life and brings out the distinctive physiography, climate, vegetation and animal life of the area. Gardner (184) studied the area in the Rio Grande Valley from Las Cruces to the mouth of the Rio Puerco which is the approximate northern limit of Larrea divaricata. He compared present vegetation with early accounts of explorers and travellers and concluded that the area was once grass covered except in certain limited areas.

Three books of general interest to the student of the southwestern deserts are: Camp-fires on Desert and Lava, which describes travel in the Sonoran Desert prior to 1909, by W. T. Hornaday (234); The California Deserts by E. C. Jaeger (245); and Death Valley by W. A. Chalfant (104). Another book, Deserts on the March by P. B. Sears (426), is interesting and valuable reading, but the title is somewhat misleading as the book deals largely with the progressive desiccation of non-arid lands.

PHYSIOGRAPHIC FACTORS AND RESPONSES OF PLANTS TO THEM

Under this heading are included: (1) the influence of topographic features -- altitude, slope and exposure, (2) soils, and (3) the reaction of underground plant parts to environmental conditions.

Topographic factors

The effects of altitude on temperatures, precipitation, and evaporation have been determined in many localities. In a brief review of variations in temperature, Tenney (499) calculated an average increase of 1°F. for each 330-foot rise, but found the rate varied with the season of the year and with local conditions. He noted, in particular, differences in the northern and southern parts of the United States. Other studies (528, 531) have shown temperature decreases of three and one-half degrees Fahrenheit for each 1,000-foot increase in elevation. South slopes at a 90° angle to the sun received one and one-half times as much heat as level areas which resulted in extreme differences in some mountain areas. Precipitation in the Colorado River Basin increased one inch on the average for each 120- to 200-foot rise, but in Utah it was found that precipitation increases might vary from one inch to each 112 feet to one inch for a 515-foot gain in altitude.

In Colorado, Robbins (388) found an inch increase in precipitation for as little as 200 feet to as much as 1,200 feet in elevation. An increase in elevation of 1,000 feet decreased mean annual temperature 2.5° F., spring 3.5° F., summer 3.0° F., fall 2.5° F., and winter 1.5° F. Increases in elevation also changed the relation of temperature between summer and winter, day and night, and sun and shade.

In his comprehensive report on the Santa Catalina Mountains of Arizona, Shreve (456) gave a full description of climatic changes due to

elevation and exposure. He briefly summarized his observations as follows:

> The higher mountains of the desert region exhibit strong gradients of change in climate and in vegetation. Both of these gradients are much more pronounced than those of mountains of equal elevation in more humid regions. They lead from arid to humid, or at least semi-humid, conditions of moisture, and from sub-tropical to temperate conditions of temperature; from low, open microphyllous and succulent desert, through a sclerophyllous semi-forest to heavy coniferous forest.
>
> The principal features of altitudinal climatic change are: the shortening of the frostless season, the lowering of the daily curve of temperature throughout the frostless season, the increasing of the intensity and duration of all critical phases of low temperature during the frost season, the shortening of the arid fore-summer (the critical season of aridity), the increasing of precipitation and therefore of soil moisture, and the decreasing of evaporation.

In another paper, Shreve (454) pointed out the marked difference in minimum temperatures for ridges and valleys. The same minimum temperature might be recorded 2,500 feet lower in a valley than on an adjacent ridge. Based on these observations, he believed that the lower distribution of plants was determined by soil and atmospheric aridity while the upper distribution of desert plants was attributable to temperature factors. Shreve (462) observed that soil temperatures decreased with altitude and the difference in soil temperatures on north- and south-facing slopes increased with elevation. Robbins (388) noted similar relationships in the cooler climate of Colorado. Shreve (462) concluded that the temperature of the soil was of less importance than the ratio of evaporation to soil moisture in determining the alternation of vegetation on opposed slopes at different altitudes. Daubenmire (149) related soil temperatures to the distribution of trees in the Rocky Mountains and reached the conclusions that all trees can withstand soil and air temperatures greater than reached in their normal range, but that the period they could stand soil drought seemed to be the determining factor.

Shreve (461) also found that other soil factors exerted a strong influence on the vertical distribution of plants. Desert mountain ranges of similar geologic structure have essentially the same vegetation (460), and differences in vegetation are associated with elevation and exposure. However, where soils were derived from different materials, Shreve (461) observed that the lowest absolute elevations were reached by encinal (live oak communities) and forest on soils derived from gneiss and granitic rocks, and desert forms correspondingly attained lower elevations on soils derived from these rocks. Vegetation ranged higher on soils from volcanic rocks and highest on limestone. He believed the chief difference among these formations was in water relations -- the penetrability, water-holding power, and capacity for losing water by evaporation.

Blumer (59) listed the vegetation from the desert zone to the spruce zone at the top of the Chiricahua Mountains in southern Arizona and compared

the zonal elevations with those reported by Merriam (317) for the San Francisco Peaks. Blumer found that zones extended lower in the Chiricahuas in spite of the fact that they are located farther south. He attributed the difference to the lower base level of the area adjacent to the mountains. In the same study, he noted that slope and exposure made for sharp differences in vegetation. In the Rincon Mountains of southern Arizona, Blumer (60) observed that there was a considerable difference between climatic conditions on the east and west slopes. The Rincon Mountains are the first high elevation in the path of the dry prevailing westerlies. As a result, evaporation is much higher on the western side. According to Blumer, the east side practises water economy while the west side spends it recklessly. Blumer (58) was impressed with the constancy of Lippia wrightii in choosing a steep and more or less rocky surface as a habitat, and its variability as to choice of aspect as governed by altitude. At an elevation of 3,000 feet and under, which is probably its lowest limit, it grows only in more or less protected places of north aspect but loses its aspect preference at altitudes above 5,000 feet. At 6,000 feet and over, it is just as definitely limited to southerly exposures. In a later paper, he (61) discussed the distribution of vegetation and the changes that occur on different slopes with gain in elevation.

In southwestern Texas, Cottle (136) found the water content of the soil 5 to 16 per cent lower on south-facing slopes and the evaporation 24 to 44 per cent higher, soil temperatures 10° to 20° F. higher at the two-inch depth, relative humidity 5 to 11 per cent lower, and wind velocity greater on a south slope than on a north slope. As a result, vegetal cover was less than half as great and production of dry matter only one-twentieth of that on the north slope. In the same region, York (599) noted similar variations in physical conditions and correlated these with the vegetation.

Palmer (351) made a survey of the ligneous flora of the Davis Mountains in Texas. These mountains are entirely made up of igneous materials. The soils are acid, porous and intermingled with rock fragments and gravel. Average precipitation is about 20 inches, occurring mostly in summer and autumn. Temperatures drop to 0° F. and below with light snows in winter. The vegetation varies from desert grassland at the base to "Canadian" species at the highest elevations. Blair (50) recognized two life belts in the Davis Mountains. The "plains life belt" lies mostly below 5,000 feet and includes seven associations: short grass, short grass yucca, short grass mesquite, mesquite-cholla, streambed, cottonwood, and riparian meadow. The "roughland life belt" above 5,000 feet includes six associations: oak-juniper, pinon-juniper, catclaw, grama-bluestem, streambed and riparian-oak. Hinckley (226) gave especial attention to the vegetation of the lava canyon region of the Davis Mountains and considered the vegetation to be a southern extension of the Rocky Mountain vegetation. He (227) also studied the vegetation of the Sierra Tierra Vieja in Trans-Pecos Texas and noted the differences in vegetation between the eastern grassland side and the western desert side.

Fosberg (179) studied the vegetation in a transect across the Rio Grande Valley in southern New Mexico and noted the distribution of vegetation as related to parent rock materials. He found that Larrea flourished where drainage was good, and that its best development was on limestone alluvial

fans and recent volcanic flows. On porphyritic hills, stunted Larrea was almost the only plant. On the flat grasslands, the transition to desert shrubs was broad except along lines of limestone or porphyritic alluvium where Bouteloua eriopoda was growing. In reporting on a similar study, MacBride (285) described the geology and ecology of the Alamogordo Desert. He noted that creosotebush marked the limits of talus slopes, and that over a long period of time, no changes had taken place on malpais. He also pointed out that the vegetation of the White Sands is precedent and is determined by physical conditions rather than chemical.

Hanson (204) made a comprehensive study of the vegetation of northeastern Arizona as related to physical factors. He divided the semi-arid and arid portions of the area into: sagebrush, below 5,200 feet; grassland, 5,200 feet and above; and woodland, 5,600 to 6,800 feet. The southern extremity of sagebrush (Artemisia-Atriplex association) is found in this area where rainfall in the driest part is about seven inches and occurs mostly in summer. The grassland belt, which is about 10 miles wide, belongs to the desert plains association and is dominated by Bouteloua eriopoda, but at the upper edge, Bouteloua gracilis becomes dominant as woodland is entered. The woodland zone, 5 to 10 miles wide, is dominated by Juniperus monosperma, Pinus edulis, Bouteloua gracilis, Chrysothamnus bigelovii and Artemisia tridentata. Benson (38) pointed out similar vegetal relationships on and near Navajo Mountain along the Utah-Colorado line. However, he found Coleogyne and sagebrush were much more important features of the vegetation.

In a botanical survey of San Jacinto Mountain in California, Hall (199) reported that the soils were derived from granite, rich in potash but low in humus. He discussed factors affecting plant distribution and pointed out that the south slopes at 45° receive nearly one and one-half times as much heat as level lands, and that hot, dry desert winds from the east and northeast carry life zones higher. A somewhat similar study was made by Bauer (31) in the Tehachapi Mountains. He described and gave detailed characteristics of the desert woodland, conifer forest, grassland and chaparral. He also pointed out the effects of altitude and exposure in determining the distribution of vegetation.

The effect of physiographic features, such as slope, exposure, physical and chemical nature of soil in favouring ligneous growth, has been recognized in many localities. Pearson (358) believed the western portion of the grassland area is treeless because of climate but that trees, once established, would continue to grow. On the basis of greenhouse trials, White (584) showed definitely that the early development of both conifers and hardwoods was adversely affected by some inherent deficiency of prairie soils. Virgin soils were deficient in available phosphorus and potassium, but this lack may not be the answer as fertilized prairie soils produced less than half as much tree growth as was obtained on untreated forest soils. Ramaley (377) found that the line between shrubs and grass and between trees and grass in Colorado was determined by soil texture. Livingston (281) stated that the extension of the Black Forest out into the plains of central Colorado was because of the presence of coarse-textured soils, and Kellogg (258) found that forests which once yielded ponderosa pine trees up to four feet

in diameter extended from the west on poor sandy soils and rocky ground well into Nebraska.

In neighbouring Kansas, Albertson (6) observed that red cedar (Juniperus virginiana), near its western limit on the Plains, is usually restricted to north-facing slopes where limestone layers outcrop or to stream banks where some protection from heat and drought is afforded.

That chemical characteristics can determine tree distribution has been pointed out by Billings (47) who found Pinus ponderosa and Pinus jeffreyi growing on hydrothermally altered volcanic rocks within sagebrush and pinon-juniper climax associations. The soils were deficient in phosphorus and nitrogen and were very acid (pH 3.5 to 5.5). Sagebrush would not grow on these volcanic soils in the field or in the laboratory.

Soils

In the early 1920's, the present concepts of soil genesis and classification were beginning to emerge in the United States. Marbut (306) outlined the beginnings of soil classification stressing the point of view that while soils have "geological origin", they are products of various forces. He recognized the line of "carbonate accumulation" and used it as a starting point in his discussion of the soils of the Great Plains (307). Marbut was also responsible for bringing the work of Russian pedologists to the attention of the American scientists through his translation of Glinka's (193) treatise on the great soil groups of the world and their development.

Sweet and Hockensmith (491) observed that soil development in semi-arid regions was dependent upon precipitation, temperature, length of season, vegetation, humidity and air movements. They believed that the zone of lime accumulation, ranging from small deposits to thick beds of caliche, was the best index of the stage of development. In the Plains area, soils vary from Chernozem-like with light lime accumulation to reddish-brown soils with highly developed caliche in Texas, and to greyish-brown soils with caliche a few inches below the surface in New Mexico.

Applying the modern soil classification to the semi-arid region of the United States, Thorp et al. (511) outlined soil zones in relation to Thornthwaite's (507) climatic provinces. The Chernozem soils and some of the Chestnut soils lie within the belt of dry sub-humid, the western part of which follows the western boundary of Chestnut soils in some places and lies considerably farther east in other places. Thornthwaite's semi-arid belt embraces all of the zone of the Brown soils, and, in addition, a small area of Sierozem soils in southeastern Colorado. The tall grasses are characteristic of the Prairie and Chernozem zones, the mid grasses of the Chestnut zone and the drier parts of the Chernozem zone, and the short grasses are most characteristic of the Brown zone.

In southwestern Saskatchewan, Hubbard (235) found, under a semi-arid climate with an average frost-free period of 120 days, that Brown soils with calcium carbonate were the rule. He also noted a highly significant correlation

between Agropyron smithii and the clay content of the soil, and a significant negative correlation between Bouteloua gracilis and per cent of clay.

In southwestern Wyoming, Glassey (190) observed that for grey desert soils, the precipitation averaged 10 inches and for light brown soils, 15 inches. Podzols were developed where average precipitation was 20 inches or more. Thorp (510) also reported similar relations for northern and northwestern Wyoming. Martin and Fletcher (311) compared the vertical zonation of soils on a mountain in southern Arizona with the great soil groups and noted remarkable similarities. They also noted that with increased elevation the volume weights decreased while total porosities, moisture equivalents and water-holding capacities increased. pH also decreased with elevation while organic matter increased. Carter (99) and Carter and Cory (100) described the soils of Texas as related to climate and vegetation. In the semi-arid Trans-Pecos portion, the soils fell mostly into the light brown and brown groups with the characteristic carbonate layer. In California, Storie (488) found grassland soils more basic with depth while timber soils became more acid. He believed that soils from igneous and some sedimentary materials may support grass under higher rainfall because of the higher carbonate content which takes longer to be leached out.

After making a study of soils in the very dry Mojave Desert, Nikiforoff (343) suggested that they might be neither Pedocals nor Pedalfers but a third type of very low biological pressure. He found that in the alluvial fans the upper portion of the profile was hardly touched by a soil-forming process. Typical desert soils are almost wholly inorganic or humusless.

In the application of soils information to ecological and economic fields, Weir and Storie (577) and Storie (487) have worked out a rating for California soils based on series and type for various areas. Their rating system considers three general factors: A. character of the soil profile; B. texture; and C. modifying conditions. A score card has been worked out for each of the factors and an "index for rating soils" is used to express relative productivity on the basis of A x B x C with 100 per cent as high. Gardner and Retzer (186) have suggested that similar relations are to be found on forest, range and watershed lands, but information for classification is insufficient at the present time. And according to Kellogg and Ableiter (257):

> Any plan for land classification or utilization, which is not based on a scientific classification of the soil, is likely to be of questionable value for any practical use where growing plants are concerned.

The organic matter and nitrogen content of grassland soils, in particular, in the semi-arid and arid areas have been given considerable attention. In a study covering the State of Nebraska, Russell and McRuer (402) found that texture is the outstanding factor in determining nitrogen in any soil type. However, in homogeneous types, nitrogen content varies with rainfall and topography -- level types containing more nitrogen than

rolling types under the same precipitation. Shively and Weaver (447) determined the volume of roots in a volume of one-half square metre in area and 10 cm deep at five stations from southwestern Iowa (true prairie) to eastern Colorado (short grass) under precipitation ranging from 33 to 17 inches. Their results showed a decrease in weights of roots from east to west, a significant decrease in organic matter, and a very significant decrease in nitrogen. Animals also contribute to soil humus for they add excreta and, eventually, their bodies (497). They may work the soils and promote aeration, or consolidate soils by trampling, and in many ways make their way felt. Along with the microfauna and microflora, the influence of the smaller animals is too often overlooked.

Jenny (246, 247, 248), who has made outstanding contributions in the field of soil nitrogen, showed (247) that the average nitrogen content of grassland soils increases logarithmically with humidity factors; and (246) that for each fall of 10° C. in annual temperature, the average nitrogen and organic matter of soils increases two to three times, and within the Great Plains, the carbon-nitrogen ratio seems to become somewhat wider with decreasing temperature. In his book, Factors of Soil Formation, Jenny (248) consolidated the results of various studies and made additional interpretations. He pointed out that scarcity of vegetation, rather than rapid decomposition, is responsible for the low nitrogen level of the western Great Plains; and that soils of drier regions are, in general, richer in soluble constituents and plant food than those of humid zones where losses by leaching are greater.

In a general review of soil moisture in relation to plant growth, Kramer (266) discussed soil characteristics, soil moisture classification and measurement, types of soil moisture, availability of moisture, and other related items. He included a bibliography of 108 titles. Much of his discussion applies to semi-arid and arid conditions.

Texture of soil becomes increasingly important in water relations as precipitation becomes less. Hardy (212) found this to be particularly true in southwestern Utah, and Marks (309) showed the distribution of vegetation in the desert area of southwestern Arizona and southeastern California was closely related to textures and salt content of the soil. On the other hand, McBryde (296) found that the Carrizo sands provided a rather uniform habitat under a range of annual precipitation from 21 to 45 inches. Under desert conditions, Baver and Harper (33) found that the average per cent of aggregation was small and that there was a close correlation between the amount of aggregation and the amount of organic matter present.

In studies near Fort Collins, Colorado, under an average rainfall of 15 inches, Hanson and Smith (209) found that tall grasses such as porcupine-grass, sleepy-grass, wildrye and western wheat-grass grew well on deep loam and clay soils, providing moisture penetrated deeply enough; and that the short grasses -- grama-grass, buffalo grass and ring muhly -- were dominant on compact soils with moisture depths of 6 to 24 inches during part of the growing season. A thin stand of grama-grass and ring muhly indicated a shallow, well-developed hardpan structure. Cole and Mathews (122) found sub-soil moisture may build up in the root zone under semi-arid conditions at certain times in the year but is exhausted during the growing season.

The effect of water running over or off the land has been considered from various angles. Allred (18) reported that run-off from properly grazed short-grass range east of Colorado Springs, Colorado, was 10 per cent of 2.65 inches of rainfall in an hour. On an improperly grazed range, the loss was 29 per cent. Valentine (532) studied five types of water-spreading structures in the semi-desert range of southern New Mexico and concluded that none was effective in improving vegetal cover. Soil factors were thought to be chiefly responsible for failure, but rabbits and rodents damaged the vegetation on some sites. Hubbell and Gardner (236, 237) studied the effects of diverting sediment-laden water on range and crop land. The accumulation of sediment damaged all grasses except Agropyron smithii. Both shallow and slow deposition caused damage to Bouteloua gracilis and Sporobolus cryptandrus. Sporobolus airoides was moderately resistant. Shaw (444) defined "erosion pavement" as a surface covering of stone, gravel, or course soil particles, accumulated as the residue left after sheet or rill erosion had removed the finer soil. Wherever unprotected soil contains fragments or solid aggregates too large to be moved readily by wind or water, erosion pavement is apt to be formed. It may be found under any climatic conditions as long as the surface is unprotected by vegetation, but is most common in arid regions where, if formed naturally, it may be called desert pavement. Lowdermilk and Sundling (283) produced erosion pavement experimentally and found that as it formed the rate of erosion levelled off.

Hardpan is characteristic in soils of the Great Plains. Weaver and Crist (567) found it over much of the Great Plains at depths of 1.4 to 3 feet and varying in thickness from 8 inches to more than 18 inches. The hardpan was observed to occur approximately at the depth of normal water penetration. The roots of many native plants penetrate and extend below the hardpan.

Shreve and Mallery (473) believed that the formation of "caliche" was primarily due to the interrupted penetration of rain water under arid conditions. They found that even thin layers of caliche greatly retard upward or downward movement of water and that roots were unable to penetrate the silicified hard layers of caliche. In pot tests, creosotebush (Larrea divaricata) made best growth where caliche made up half or more of the soil mixture.

A great deal has been written about saline and alkali soils. In 1902 Kearney and Cameron (254) reported on their experiments with various salts in pure and mixed solutions and discussed the formation of black alkali. They included an extensive bibliography which was added to by Dorsey (163) who summarized available information on the formation of alkali, its source, and why it is found in arid regions. Breazeale (74) considered any water-soluble salt as alkali, and that the alkali tolerance of plants was a matter of adaptation; also, that the presence of calcium increased the tolerance of wheat seedlings for sodium chloride and other alkalies.

In 1945 Magistad (300) reviewed 362 contributions in the field of plant growth relations on saline and alkali soils. He distinguished between saline and alkali soils on the basis that saline soils have high salt contents -- at least 0.1 per cent in the case of chloride salts, and 0.2 per cent

where sulphate salts predominate. Alkali soils contain at least 12 per cent exchangeable sodium plus potassium in terms of the exchange capacity of the soil. Twelve per cent is suggested because soils containing this amount of exchangeable alkali bases have impaired physical characteristics. Gradations of saline and alkali soils are divided into four main classes: saline soils, saline-alkali soils, slightly saline alkali soils and degraded alkali soils (alkali soils with a very low salt content). A distinction is made between the characteristics of saline and alkali soils since it is believed that the physiological reactions of the plant are different under the two sets of conditions. It follows that a plant may be tolerant to one soil type and not to the other. In saline soils, the principal factor depressing plant growth is the decrease in available water due to the high osmotic pressure of the soil solution. Decreased growth due to harmful effects of specific ions may occur, but such effects are less important than the inhibition resulting from high osmotic pressure. Many reasons are listed to explain why a reduction in water intake decreases plant growth. These include: salting out of cellular proteins, shrinkage of cell contents from cell wall, irreversibility of hydrations of cell contents, and interference with ion accumulation. Plants in saline soils are subjected to high concentrations of certain salts and to salts that are not in the most favourable ratios for plant growth. Under such conditions, nitrogen compounds are not assimilated, carbohydrates accumulate, and growth rate is reduced. On the other hand, starch formation may be inhibited by high chloride concentrations. Alkali soils with large contents of replaceable sodium have unfavourable physical properties. Such soils disperse readily, do not drain well, do not take water well, and the soil air may be low in oxygen. In addition to poor physical conditions, a number of authors ascribe the deleterious effects of alkali soils on plants to a breakdown of the calcium régime. The soil solution in equilibrium with alkali soils is very low in calcium and high in sodium. In addition to unfavourable physical conditions and lack of calcium, alkali soils usually have high pH values with attendant unavailability of several essential elements such as iron, manganese, phosphates, and, at times, nitrates. In alkali soils of low salt content, some sodium carbonate is present. The alkali carbonates are very toxic and even corrosive to plant parts. However, only in extreme cases, is there any appreciable amount of free sodium carbonate.

Thorp et al. (511) stated that western wheat-grass was the most characteristic grass of the Pierre clay soils and saltgrass of Solonchak and Solonetz. Hanson and Whitman (210) agreed with this in general and gave more detail on the formation of Solonetz soils and the natural regeneration of them. Hilton (225) studied the effects of micro-ecological factors on the germinability and early development of Eurotia lanata. He found germination was not markedly affected up to 1.5 per cent sodium chloride. Above this amount the decline was sharp, and above 3.0 per cent only a few germinations were noted.

Pure gypsum, as found in the White Sands of New Mexico, is especially low in nitrogen. Emerson (171) found that seedlings became established in flats between moving dunes where the water table is two to three feet below the surface. It appeared that roots absorbed water from a saturated solution of calcium sulphate. Campbell and Campbell (93) found sparse vegetation on soils made up of 60 to 65 per cent calcium sulphate, but found that the vegetation became less sparse and included more species where quartz sands were present.

Waterfall (553) listed the gypsophilous plants of Trans-Pecos Texas and adjacent New Mexico. He found Coldenia hispidissima was the most abundant species of the desert gypsum, being as characteristic of such areas as Larrea divaricata was of the calcareous desert soils of the same region.

Reaction of underground plant parts to environmental conditions

The pioneer studies of Cannon (97) on the root systems of desert plants opened the way for a better appreciation of the importance of roots in plant development and survival. Cannon found that the roots of desert plants were remarkable for their individuality but, in the main, could be divided into three general types: (1) taproot type, (2) sub-surface lateral type, and (3) mixed type. He noted that, even in the desert, root competition was severe. Spence (480) found more fibrous-rooted plants in Idaho and suggested a grouping of root systems as follows: (1) fibrous, (2) semi-fibrous, (3) semi-taproot, and (4) taproot.

In the semi-arid region, Weaver (556, 558, 559, 560) has made outstanding contributions by his very careful studies of more than 1,500 root systems representing more than 150 species. His studies were mostly conducted in the central grassland area of the United States but included some early studies in southeastern Washington (556). He (558) observed that as a community, short grass plains species were more shallow-rooted than were those of mixed prairie, while the latter were less deeply rooted than were species of true prairie; and (559) 65 per cent of true prairie species, 42 per cent of mixed prairie species, and 13 per cent of short grass plains species had roots reaching below five feet. Weaver (560) also found that overgrazing reduced vigour of grasses, and seedlings weakened by grazing rooted less deeply and were more apt to die of drought or injury. Soils that are trampled, packed and eroded are in poor physical condition for new root formation. As a result, growth is poor, less herbage is produced, storage is less, rhizomes are weakened and, consequently, winter killing and drought and grazing losses are greater.

Root growth is decidedly influenced by soil texture. Weaver (558) found hard sub-soil layers inhibited root growth. In deep loam without hard sub-soil, roots penetrated two to three feet deeper. He indicated that root distribution, as modified by soil texture, strikingly conforms with the distribution of soil moisture and may also be conditioned by aeration. Merkle (308) found that roots would penetrate a poorly developed caliche layer that was hard when dry but soft when wet. He noted that the penetrability of the soil and its moisture content appeared to be the two factors exerting greatest influence in root development. Weaver and Clements (566) and others have found that a relatively low water content makes for greater root development.

Detailed root studies have been made by a number of investigators. Stuckey (489) gave particular attention to root growth, regeneration and longevity; Weaver and Zink (570, 571) studied seminal roots and the longevity of roots of perennial grasses; Conrad and Veihmeyer (125) worked on the relation of root development and soil moisture; and Muller (332) studied the

root system of guayule (Parthenium argentatum). He found that in its native habitat the guayule root system had a maximum depth of two to five feet, but that under irrigation it would extend to 16 feet. He also showed that guayule could not stand competition from fibrous-rooted plants (particularly grasses); hence, in its native habitat, it was limited to a narrow zone above the desert and below the desert grassland.

CLIMATIC FACTORS AND THE REACTIONS OF PLANTS TO THEM

Precipitation

In Utah, Sampson (407) made comparisons of the physical factors and growth of oakbrush, aspen-fir and spruce-fir zones. Clyde (117) made studies of the precipitation of valleys and adjoining mountains. He noted that precipitation was lightest during June, July and August, and that at Logan, Utah, approximately 56 per cent of the annual total fell during the period from October to March, inclusive. Price and Evans (375) observed the climate of the west front of the Wasatch Plateau in central Utah and called attention to the large increases in precipitation between oakbrush and aspen types. These increases were later shown by Lull and Ellison (284) to be caused in part by local conditions that unduly influenced measurements. They (284) found the relation between elevation and precipitation to be linear.

Shreve (455) and Humphrey (239) reported on desert rainfall at the Desert Laboratory. They noted great variations in a small area and that winter rains were more uniform than those of summer. Mallery (304, 305) summarized rainfall for the Sonoran Desert in two papers published in 1936. These included records from 22 stations south, southwest, and west of Tucson. He pointed out that rainfall increased with elevation and with distance from the Gulf of California. Summer rainfall became greater than winter rainfall away from the Gulf. Local spots varied greatly from storm to storm but averaged out over the season and over the years. Turnage and Mallery (524) also found that rainfall increased with elevation, but there were differences from south to north and from west to east that tended to obscure relations for the area as a whole. They observed that winter storms were similar to the western part of the United States, but that summer storms blew in at high altitudes from a southerly direction and were similar to the rainfall régime of Mexico.

Shreve (466) considered a period of 30 days without rain of more than 0.15 of an inch as a drought period. On this basis, drought periods near Tucson averaged two to seven annually, totalled 94 in 27 years, and amounted to 55 per cent of the elapsed time. He described the effect of these droughts on vegetation as follows:

> In the warm months a period of two or three weeks without rain will kill the herbaceous ephemeral plants and will check the activity of the root perennials and small shrubs. On the other hand, a period of two or three months without precipitation will be of little consequence to cacti and such deep-rooted trees as mesquite (Prosopis) and catclaw (Acacia greggii).

Watson (554) believed that moisture was the greatest limiting factor in the distribution of vegetation in the Rio Grande Valley near Albuquerque where he observed a range from 7.5 inches in the valley to 24 inches in the mountains. He noted the lower distribution of ponderosa pine was correlated with the lower limit of average heavy snow.

In the short grass and foothills areas of Colorado, Vestal (540) noted that the driest part of the plains was 18 to 25 miles from the mountains and extended over a belt 30 to 60 miles wide. He also observed that a slight difference in rainfall could be critical in the distribution of vegetation. Crowe (141) attempted to get a more realistic picture of precipitation distribution in the western Plains area by comparison of median values. He noted a primary rain period in May and June in Montana, while June was the highest month in the Platte region. The maximum occurred in May in the Laramie region, and July and August were high in the Rio Grande region.

Visher (544) showed that the ratio between average and extreme precipitation is high in the semi-arid and arid areas. He (546) also reported on the intensity and frequency of dry seasons. In another paper, he (547) considered the effects of high temperatures and the seasonal distribution of precipitation and pointed out some ecological correlations. He showed that the dry summer region was occupied by desert shrubs or western coniferous forest, the wet winter area by coniferous forests, and the dry winter area by grassland. He included a bibliography of his publications that have a bearing on ecology. Visher (545) also worked up information on evaporation. He showed that for the frost-free period in the prairie-plains region, precipitation-evaporation ratios times 100 gave a value of 60 for the approximate eastern boundary of the mixed prairie and the semi-arid region. A ratio value of 20 practically sets off the boundary of the northern and southern desert area.

Not all precipitation reaches the ground. In grassland, for example, Clark (105) found that Andropogon furcatus grassland intercepted 47 per cent of the water applied at the rate of one inch per hour; it retained up to 97 per cent of the moisture in light showers. Buffalo grass (Buchloe dactyloides) intercepted 16 per cent of the heavy showers and 74 per cent of the light showers. Other prairie plants showed similar relations, varying in accordance with the density of vegetative cover. Hamilton and Rowe (202) found that in California, interception by chaparral may be as high as 50 to 75 per cent in light rains but dropped to three to six per cent in heavy rains. Stem flow was an important item, and about 20 per cent of the precipitation reached the ground by this route.

Temperature

Soil and air temperatures in the desert near Tucson were studied by Sinclair (475) who recorded a great daily range. Buxton (88) reviewed the earlier attempts to measure surface and soil temperatures and pointed out the source of discrepancies. He was convinced that the best method of measuring surface temperature was to roll a maximum thermometer along the surface or to lay it on the surface and sprinkle it with dust or sand. Where the surface was hard, good results were obtained by using small shavings of paraffin waxes

of various melting points. Turnage (522) measured sub-soil temperatures with thermocouples and found them mild and equable when compared to surface soil temperatures of 20° to 165° F. He observed that roots in the sub-soil were in a vastly different environment from that of the superficial roots and shoots of the same plant.

Shreve (465) noted that under desert conditions, the light shade of a tree or large bush supported a greater population of herbaceous plants than grew in the open. He found that moisture conditions were not materially different, but that there was a difference in soil and air temperatures. Consequently, he favoured temperature factors to explain differences in plant growth in sun and shade. On the other hand, Went (579) thought there was more involved than the mere effect of the shrubs on physical factors. In support of this viewpoint, he pointed out that some plants were commonly associated with certain shrubs. Bonner (63) has reported that some desert shrubs, such as guayule and Encelia farinosa, may secrete toxic substances that are of significance in determining the floristic composition surrounding the plant.

Temperature also plays an important rôle in the distribution of desert plants, particularly succulents. Shreve (453) found that a single day without midday thawing, and the consequent failure of Carnegiea to warm up above freezing would result in its death. Turnage and Hinckley (523) did not find any points in the Sonoran Desert where records were available to show that such conditions prevailed. Other species of cacti, for example, Opuntia versicolor, can stand up to 66 hours of freezing, and in the mountains, small succulents are known to have withstood freezing for 13 days or more (453).

The United States Department of Agriculture Yearbook for 1941, Climate and Man (528) is a valuable source of information on climate and weather in the United States, and it provides additional material on many of the physical factors of the environment.

Response of plants to climatic factors

Adaptations to aridity. The explanation of the ability of certain plants to survive under dry conditions has been sought by many investigators; and whether or not they have found the answer or answers, they have, at least, contributed to the sum total of knowledge related to the utilization of desert areas. Shreve (457) called attention to the weight of physical factors in the study of plant distribution and conducted a series of experiments to correlate climate and vegetation with particular emphasis on arid conditions. Shantz (435) pointed out that plants have various methods of meeting drought conditions and that we should not look for the one or two physical or physiological variations to explain every case. His classification of plants which grow in regions subject to drought into drought-escaping, drought-evading, drought-enduring and drought-resisting suggests various means of meeting drought conditions. Maximov (312, 313), as a result of his comprehensive studies of xerophytes, concluded that the ability of a plant to survive in a dry environment was not because of high efficiency in water use but rather because of its ability to live under conditions of water deficiency.

The subject of life forms of plants as related to environmental conditions was reviewed by Adamson (3) in 1939. On the basis of the consideration of about 80 contributions to the subject, he believed that if we are to obtain any real expression of the reactions to environment, the underground portions of plants must be included. He also noted that physiological relations are important and that some means of correlating "behaviour" and "form" is needed. An example of this is to be found in Shantz's (435) classification of plants in relation to drought resistance in which both behaviour and form were considered. Shreve (470) reviewed all life form schemes from the beginning to that developed by Raunkiaer (379) and developed a new scheme for arid areas based on criteria used by earlier investigators. Shreve's scheme is based on duration of life, height, character of stem, amount and character of branching, presence or absence of leaves, insertion, size and seasonal duration of leaves and presence or absence of succulence in stem or leaf.

The creosotebush (Covillea tridentata, Larrea tridentata, Larrea divaricata), one of the most widespread desert shrubs and one that is found in the driest portion of the desert, has been studied as a typical xerophyte. According to Spalding (476), the creosotebush is able, through its absorbing cells, to abstract continuously a certain amount of water, however small, from such dry soil as that of the desert mesa; to maintain transpiration through many months of excessive drought; and, at the same time, to regulate nicely the amount of transpiration to correspond with the available water supply, while all the time, it is capable of living and does live as an ordinary mesophyte when given a suitable supply of water. Runyon (399) pointed out that the creosotebush thrives on abundant water, and Ashby (22) found that the leaves of the creosotebush have as many stomata per unit area as privet (Ligustrum sp.) and that the stomata do not have any special anatomical adaptations. Runyon (399) concurred and added that as a rule leaves are persistent throughout the driest seasons; that leaves which successfully endure the most prolonged and severe droughts are only partially grown -- their dormancy is not complete, and they resume growth and activity with the return of favourable conditions. He (400) found that during growth the water content of the foliage was not lower than that of many mesophytic leaves, but that during drought the water content was lower than that reported for any other seed plant. He also observed that three types of leaves were produced: a-type -- high water content, very little drought resistance; b-type -- intermediate; and c-type -- resistant to drought, lower water content, longer life span. Mallery (303) found great seasonal variation in the osmotic concentration of the leaf sap of creosotebushes. As minimum values were approached during the rainy season, there was not much variation between areas, but there was a great difference among the various habitats during drought periods.

Edith Shreve (451) described mesophytic and xerophytic leaves of Encelia farinosa, another common desert xerophyte. She (450) compared Encelia with a spring annual living near its limit of endurance and a summer annual living through temporary drought in a wilted condition from which it easily recovered. In her investigations on paloverde (Parkinsonia microphylla), she (448) noted four adjustments to drought: (1) leaflets close a little earlier each day, (2) transpiration amount is lessened with the drying out of the

soil, (3) the leaves drop off and later the rachises, and (4) twigs and small branches die and finally the whole limb.

Spalding (477) found that the leaves of some desert shrubs absorbed water and others did not. The leaves that were more xerophytic in structure appeared least capable of taking up water through their leaves.

Succulence, as an adaptation to drought or as a consequence of drought, has been investigated by MacDougal and associates (291, 292, 293), Livingston and Brown (279), Edith Shreve (449), and others. The studies are in general agreement that succulence is a result of the conversion of polysaccharids into pentosans and mucilages, induced by lessened water supply in the cells. All agree that succulent plants can remain alive for long periods (up to several years) without any additions of water.

The ability of plants to take up water has been considered in the broader aspects by Kramer (267) on the basis of a review of 273 contributions. He recognized two kinds of absorption: "active", when soil moisture is abundant, resulting in a built-up pressure within the plant; and "passive", when transpiration is rapid and soil moisture is deficient, resulting in simple absorption by the roots. Magistad and Breazeale (301) concluded that the plant could maintain moisture equilibrium at the wilting percentage by exuding water from its roots, and Breazeale (75) believed that plants are able to draw nutrient materials from a soil which is maintained at the wilting percentage, while Breazeale and Crider (76) concluded, from experimental "pot" studies and observations, that the roots of certain plants are able to penetrate soils that are below the wilting point and are able to absorb moisture from one soil horizon where it is available and transport the moisture and exude it into another soil horizon where it is scarce. Daubenmire and Charter (153) found the wilting percentage of soils has essentially the same significance for woody legumes as for wheat. The woody legumes stopped growing at the wilting percentage but did not wilt.

The relation of density of cell sap in relation to environmental conditions has been extensively studied by Harris and his associates (216, 217), Livingston (278), Mallery (303) and Korstian (265). The general relation of density of cell sap to environmental conditions was summed up by Korstian (265) as follows: (1) annual herbaceous species which complete their life cycle before critical dry season have low sap densities; (2) concentration of sap of woody species is much higher than that of herbaceous species; (3) highest sap densities occur on the most adverse (dry or saline) sites; (4) thick leaf with compact structure and thick epidermis tend toward lower sap concentration; epidermal coverings and hairs make for lower densities; and (5) greater sap densities are generally found in the more drought-resistant species. Korstian also included a bibliography of 121 titles.

The influence of transpiration on the temperature of leaves of crop plants was investigated by Miller and Saunders (323). They found that the temperature of a leaf is influenced by the temperature of the air, by available water supply in the soil, by air currents, by the type of leaf, by the intensity of light to which it is exposed, and by other factors. In California chaparral,

Copeland (130) found that transpiration resulted in the cooling of leaves up to 10° C. and that some of the most actively transpiring plants gave off water at a rate representing two feet of water per unit of leaf area for the active growing season. Edith Shreve (449) reported the transpiring power of cactus is greater at night than during the day.

Another phase of water relations, the water requirement of plants, has been intensively studied by Briggs and Shantz (77, 78, 79, 80). In their first publication (77) released in two parts, the second part was devoted to a review of pertinent literature. They defined water requirement as ". . . the ratio of the weight of water absorbed by a plant during its growth to the weight of dry matter produced". Their early results showed that alfalfa used four times as much water as millet and the more efficient sorghums in the production of a pound of dry matter; corn ranked next to millet and the sorghums in efficiency; and small grains had a medium water requirement or about one-half that of alfalfa. Comparison of results between Akron, Colorado and Dalhart, Texas, showed about the same requirement for sorghum, but for wheat it was 35 per cent higher in Texas, indicating that wheat is relatively better adapted to Colorado conditions. In later studies, Briggs and Shantz (78) and Shantz and L. Piemeisel (439) showed that amaranths, buffalo grass, grama-grass, purslane, and Russian thistle have a low water requirement and compare favourably with sorghum and millet; while sunflower, western ragweed and western wheat-grass have a higher water requirement about equal to that of alfalfa. In detailed studies of daily transpiration at Akron, Colorado, Briggs and Shantz (79) found the loss of water from plants was about 5 to 14 per cent of the loss from a free water surface of equal area. During a 10-day period, small grains transpired 12 to 16 times the dry weight of the crop, sorghums 6 to 9 times and alfalfa 36 to 56 times. A comparison of the water requirement of different plants during three years (80) brought out different reactions to climate and weather. High fertility reduced water requirement, but the amount of moisture had little bearing as long as water was available. Dillman (160) conducted similar studies in the northern Great Plains and reported approximately the same results. He also found that western wheat-grass had a high water requirement; that bromegrass and crested wheat had a lower requirement, but even so it was about twice that of wheat. McGinnies and Arnold (299) determined the water requirement of 28 species of Arizona range plants. They found that summer annuals were very efficient -- winter annuals, less so. Grasses showed considerable variation but on the average were three to five times as efficient as shrubs. Following a slightly different approach, R. J. Weaver (572) measured the water usage of native grasses by sod transplants in mowed and unmowed prairie near Lincoln, Nebraska, and found that water loss (transpiration plus evaporation from the soil) averaged 55 to 80 per cent as much in pasture as in prairie. In their studies on the consumptive use of water by native plants in moist areas in southern California, Blaney and associates (56, 57) found that these phreatophytes transpired large quantities of water.

The production of viable seeds and the germination and establishment of seedlings in semi-arid areas are subject to environmental influences, but at the same time, certain patterns of reactions are to be found in the more common plant species. Branson (69) reported that the production of

grass seed during the drought of 1939 in Kansas was correlated with soil moisture during the period of flowering and seeding. Jackson (244) likewise found that the amount of rainfall during the growing season affected germination of desert grassland grasses. Blake (55) observed that the average germination of prairie grasses in the greenhouse ranged from 10 to 20 per cent. Toole (519) showed that dropseed grasses germinated better at high or alternating high and low temperatures. Tolstead (515) divided grasses into three groups according to their germination characteristics: (1) requiring low temperature treatment, (2) not requiring low temperature treatment, and (3) winter annuals that germinated in the fall. Glendening (191) found that soil moisture was the major controlling factor in the germination of Heteropogon contortus. Working with 10 native plants in the desert grassland, he (192) also reported that increasing the litter cover increased soil moisture and resulted in the emergence of 4 to 20 times as many seedlings as from bare soil.

Olmsted (345, 346) studied the relation of Bouteloua curtipendula to water supply and to drought by growing it in crocks in the greenhouse and found that the variations in moisture affected the height of the plants more than they did the number of parts. Seedlings that failed to survive drought had failed in the establishment of adventitious roots. He (347, 348, 349) also investigated photoperiodic responses for six species of grama and for strains and clonal divisions of sideoats grama (Bouteloua curtipendula). All of the grama-grasses were definitely sensitive to photoperiod, and geographic strains of sideoats grama showed unusually strong response to photoperiod differences. Weaver and Zink (570) and McAlister (295) also studied the effects of drought in greenhouse studies and gave additional evidence to show the importance of root establishment in the endurance of drought. These studies were corroborated by Plummer (369) who found that root development prior to summer drought was the most important factor in survival. Weaver and Mueller (569) concluded that the restoration of ranges from drought was a slow process because of the scarcity of seeds and the hazards of growth. McAlister (295) pointed out that even very drought-resistant plants, such as Agropyron smithii, may have very low drought resistance as seedlings.

The germination of seeds and the establishment of plants on deserts (the warmer deserts in particular) have been given considerable attention by various investigators. Possibly the most interesting problem has been why the seeds of some plants germinate only in cool weather and those of others only in warm weather even though moisture conditions may be favourable in both the cool and the warm seasons. Thornber (502, 504) noted this seasonal relationship and found that the seeds of winter annuals would germinate in an icebox in summer. He (503) listed about 150 winter annuals in the vicinity of Tucson and a third as many summer annuals. No annual species were found growing in both seasons. Went (581) subjected soil from the desert to artificial rain and controlled temperatures and observed that only summer annuals germinated under warm temperatures and only winter annuals under cool. In Death Valley, Went and Westergaard (582) noted that a rain followed by temperatures of 30°C. resulted in no germination, that after a rain followed by temperatures of 15° to 16° C. only Larrea germinated, and with temperatures of 8° to 10° C. winter annuals but no Larrea germinated. On the basis of his

observations, Went (580) divided the vegetation of the Mojave Desert into five groups according to germination and period of growth: (1) summer annuals, (2) winter-germinating spring annuals, (3) summer-germinating spring annuals, (4) plants unrestricted in germination conditions, and (5) shrubs (almost all summer germinators). Barton (28) found a rest period was necessary for most winter annuals and that comparatively low, or a combination of high and low, temperatures were necessary for germination.

Livingston (276, 277) noted that the driest period of the year occurred just before the summer rains; that germinating seedlings of desert plants produced roots rapidly and tops slowly; and that the loss of water by evaporation from soil was reduced by the formation of a natural mulch in the surface soil. Shreve (459) observed that after summer rains, germination commences very promptly and growth proceeds with great rapidity. On the second morning following the first heavy rain, it is possible to see germinating activity, and on the third morning seedlings can be identified. He also noted that very few seedlings survive through extreme climatic conditions and competition; so only an occasional plant remains to replace the older perennials. Went (580) agreed with Shreve and added this observation:

> The spacing of shrubs is rigorously controlled in the desert and ultimately only one new shrub can become established for every one which dies.

The ability of mesquite seeds to remain viable was observed by Martin (310) who found that after 44 years on an herbarium sheet three out of five seeds germinated. According to Paulsen (354), the mortality of mesquite seedlings from causes other than drought may be high. Mortality after 15 months was 47 per cent when seedlings were protected from cattle and rodents, 94 per cent when protected from cattle only and 96 per cent when subjected to grazing by cattle and rodents.

<u>Effects of droughts</u>. Albertson and Weaver (9, 10, 11) and Weaver and Albertson (561, 562, 563, 564, 565) made detailed studies of the effect of drought in the central grassland area. According to Albertson and Weaver (9), the drought between 1933 and 1940 was the most severe ever recorded in the United States. In one area, all of the little bluestem and half of the big bluestem was killed by the drought of 1933. Blue grama, buffalo grass and 15 deep-rooted forbs remained. Some areas were covered with dust to a depth of 2.5 inches, and according to the authors (11) ". . . Drought and dust unaided by grazing had reduced a sample area of mixed prairie centuries old to a disclimax of short grasses". In another case (565), they reported that pre-drought sod of about equal amounts of buffalo grass and blue grama was replaced after the drought by one with two-thirds buffalo grass and one-third blue grama, but in thinner, drier soil, blue grama finally composed about three-fourths of the cover. Where pre-drought cover was formed of 45 per cent little bluestem and 17 per cent sideoats grama, the post-drought cover contained 3 per cent little bluestem, 66 per cent sideoats grama and 21 per cent short grasses.

Runyon (401) estimated that three-fourths of an inch of dust or approximately 86 tons per acre was deposited by a single severe dust storm.

He tested dust samples for germination of included seeds and found that most of the seeds that germinated were from weedy plants.

Albertson and Weaver (10) also reported high losses of trees in the prairie climate. Losses were high throughout the area, but were particularly high in the west where soil moisture became exhausted for prolonged periods. Grass competition and grazing were factors in the deterioration of woodlands. Weaver and Albertson (561) reported in 1936 that the water content of the soil was exhausted to 3.5 to 6 feet at Hays, Kansas, during the drought years 1933-1935. Day temperatures rose to 86° to 97° F., relative humidity was low, and severe conditions were augmented by high winds. As a result, Andropogon scoparius lost up to 90 to 100 per cent where it was mixed with short grasses. At Phillipsburg, the mixed prairie was temporarily converted into pure short grass by the death of the bluestems and other tall grasses. Three years later, they (562) noted additional results of continued drought. Little bluestem (Andropogon scoparius) showed the greatest depletion even in true prairie; Stipa, Koeleria, Sporobolus, and Agropyron developed nearly pure stands to replace former vegetation; Bouteloua curtipendula and Agropyron smithii showed great aggressiveness; Stipa spartea and Sporobolus heterolepis gained new territory; and Bouteloua curtipendula became a dominant species. A study of 88 representative ranges in the mixed prairie area made by Weaver and Albertson (563) showed great reductions in grass cover. "At the end of the great drought. . ." they (564) found that Andropogon scoparius suffered the greatest loss; Sorghastrum nutans all but disappeared from the uplands and decreased in the lowlands; Poa pratensis almost all died out in pastures and drought-stricken prairies; Sporobolus heterolepis and Stipa spartea were more abundant than before the drought; and Bouteloua curtipendula almost disappeared from the short grass but gained in areas left bare by loss of little bluestem. They (565) also noted that Bouteloua curtipendula and Koeleria cristata became important dominants; buffalo grass entirely disappeared from some ranges and remained alive only in the best watered places; blue grama suffered less severely and gained on some hillsides; and sand dropseed, sparse before the drought, increased greatly during later drought and thereafter.

According to Rogler and Haas (394), Stipa comata made up the major portion of the forage before the drought of 1933 in the mixed prairie type near Mandan, North Dakota. After the drought, Agropyron smithii was the major component. Ellison and Woolfolk (167) observed decreases in density from 1933 to 1935 amounting to 78 per cent for Bouteloua gracilis, 75 per cent for Agropyron smithii, 79 per cent for Buchloe dactyloides, 62 per cent for Stipa comata, and 12 per cent for Carex filifolia. During the same period, Poa secunda showed an increase of 179 per cent. At Hays, Kansas, Savage and Jacobson (422) recorded losses due to the heat and drought of 1933-1934 of 74.8 per cent on closely grazed and severely trampled areas, 64.6 per cent on moderately grazed areas, and 44.4 per cent on unwatered lawns. They found a direct positive correlation between closeness of clipping for one year and survival from drought.

Julander (253) found that food reserves were essential to heat and drought resistance and that heavily grazed grasses did not accumulate reserves and were therefore less resistant to heat and drought. Reitz and Morris (381)

believed that overgrazing for one season is probably no more serious than one year of drought, but if either is extended over a series of years, significant depletion results; and when combined, impoverishment is hastened. Clements et al. (116) found that leaf area and dry weight were greatest when both water and nutrients were available in adequate amounts and lowest when both were deficient. Light was less important because usually there was enough for photo-synthetic needs. Water was of greatest importance. Taylor (496) expressed a similar observation in his restatement of Leibig's Law of Minimum in which he pointed out that:

> The growth and functioning of an organism is dependent upon the amount of the essential environmental factor presented to it in its minimal quantity during the most critical season of the year, or during the most critical year or years of a climatic cycle.

Savage (420), in speaking of the drought of 1932 to the late spring of 1935 in the central and southern Great Plains, stated that:

> High temperatures undoubtedly represented the most damaging climatic factor, as indicated by high plant mortalities recorded even in localities where precipitation was not much below normal. Drought in the form of limited rainfall ranked second in damaging effects and seriously aggravated the injury caused by high temperatures, hot or erosive winds, and overgrazing.

Savage also reported that the surviving grass cover was usually less on moderately grazed pastures than on an ungrazed area, andthat losses were greater with heavier grazing where the drought was severe. Blue grama was injured more than buffalo grass by heavy grazing but less injured than tall grasses. Riegel (384) pointed out that blue grama, which tends to form sods in the north and bunches in the south, resists freezing and drought by becoming dormant. Its resistance is decreased by long droughts and overgrazing. Whitman et al. (589) made a study of the effects of drought in the mixed prairie of southwestern North Dakota. They found that sedges were not reduced by drought, that Junegrass was reduced about one-third, and other grasses from one-half to two-thirds. Little bluestem decreased by 74 per cent. Annuals became abundant and remained high following the drought, and blue grama and western wheat-grass made rapid recovery to pre-drought level.

Pechanec et al. (359) recorded the effects of the 1932-1935 drought on the Snake River Plains, Idaho. They noted that not only was precipitation low during the drought period but also that temperatures were higher. Perennial grasses lost more than a third of their 1932 density -- Agropyron spicatum and Stipa comata were particularly weakened. Annual weeds were almost completely absent in 1934 but present in profusion in 1935. The density of shrubs decreased 46.8 per cent of their 1932 density in 1934.

The rise and decline of the prickly pear with changes in weather has been noted by Timmons (512). In the dry years of the 1930's, with the aid of

jack-rabbits in disseminating the seed, it spread to four million acres in Kansas. In the wet years of 1940-1942, prickly pear rapidly deteriorated and disappeared in many localities. Turner and Costello (525) found that the plains prickly pear (Opuntia polycantha) was favoured by periods of drought. Its shallow extensive roots made possible the use of water from light showers. Grazing had little influence -- prickly pear increased on both overgrazed and protected areas. During moist years, it appeared to be particularly susceptible to insects and disease and lost ground rapidly. Cook (126) considered drought to be the controlling factor between prickly pear cactus and insects, but proper grazing had an indirect influence by providing a more favourable habitat for insects. In Clay County, Kansas, Schaffner (424) observed that as the grasses were weakened from overgrazing, prickly pear (Opuntia macrorhiza) spread rapidly from its original position in the less favourable habitats.

The question of past climates in the semi-arid and arid areas and whether they were wetter or drier has been given considerable attention by various scientists. Some prominent geologists maintain that much of the present erosion is due to the fact that the region is experiencing a dry cycle. Many biologists, on the other hand, contend that the evident accelerated erosion is due to loss of plant cover because of overgrazing, fire or other man-induced causes. Sears' (427) excellent review of the evidence for and against the "xerothermic theory" as applied to past climates provides a good background for the consideration of climatic variations. As a result of their observations near the Davis Mountains in Texas, Bryan and Albritton (83) contend that dry periods are the cause of erosion. They discuss characteristics of soils and soil conditions that can be used to provide paleoclimatological data. The particular soil in the Davis Mountains, the authors believe, records three stages of relative aridity during which caliche was deposited in the sub-soil, and two intervening stages of moister climates during which caliche was partially or completely dissolved. Adjacent valleys are underlain by three bodies of alluvium separated by erosional disconformities. They believe deposition took place in humid times whereas erosion took place in arid times. They claim we have been in a dry period since 1880. On the other hand, Rich (383) who made observations in southwestern New Mexico some thirty years earlier, discussed trenching on the basis of former stabilization due to heavy grass cover and recent loss of cover. Thornthwaite et al. (508, 509) felt there was no evidence to support the theory of increasing aridity. A land surface irritated by overgrazing and cut by stock and wagon trails will be gullied by a less intense rainstorm than will a surface in its natural condition. Most of the storms that contributed to the extensive gullying of the last half century would have done little or no damage had the surface remained in its natural condition. Cooperrider and Hendricks (129) made comparisons of vegetation, soils, and erosion under both good and poor land management in the upper Rio Grande Valley. In their opinion, the theories that climatic and geologic changes have caused acceleration of erosion are untenable. They collected historical evidence which showed that the recent general decline of watershed lands and resources began during the 1880's following the impairment of the natural vegetation cover which was caused principally through overgrazing and also through wanton timber cutting, man-caused fires, promiscuous wagon trailing and dry farming.

ECOLOGICAL EFFECTS OF GRAZING AND CLIPPING

Over the years, the science of range and pasture management has developed as an application of ecology. The early studies, such as those of Bentley (39), Vasey (534) and Thornber (504), were largely descriptive. But following the leadership of Sampson (406, 407, 408), workers in the field of range management became increasingly aware of the science of ecology and its application to the science and art of range management. This development is very well shown in Stoddart and Smith's (486) and Sampson's (412) textbooks on range management, and by Whyte (592) in his review of organizations engaged in range management.

Effects of grazing

The ecological effects of grazing have been studied throughout the semi-arid and arid areas of North America. They cannot be entirely separated from the effects of droughts and other weather factors as variations in grazing frequently occur independently of weather variations and it is often impossible to tell what changes are due to grazing and what to other causes. Because it has not been possible to control the weather, most grazing studies have considered it as one variable, and studies of the effects of grazing are often also studies of the effects of climatic factors on the vegetation.

Clarke et al. (109) studied the effects of climate and grazing on short grass vegetation in southern Alberta and southwestern Saskatchewan under precipitation of less than 11 inches. They found in this short grass phase of mixed prairie that soil moisture was the limiting growth factor. Moderate grazing tended toward slightly greater proportion of short grasses to mid grasses and a slightly greater cover of unpalatable weeds than were found on ungrazed areas. Moderate grazing, while intensifying the effects of drought, appeared to be less important than climate in modifying the plant cover. The influence of heavy grazing was as great or greater than the effect of drought. Sarvis (417, 418) found that native grasses deteriorate when grazed because of (1) too early grazing, (2) continuous grazing, and (3) overgrazing. Both Sarvis and Clarke et al. found rotation grazing superior to continuous use. However, Hanson and Love (208) found no decisive differences between continuous and deferred and rotation grazing in Colorado.

At Mandan, North Dakota, Rogler and Haas (394) found a highly significant correlation between fall moisture in the surface three feet and surface six feet and native forage production the following season. Above average precipitation from April to July was accompanied by above average yields 70 per cent of the time. When precipitation was below average, yields were below average 100 per cent of the time. Sarvis (417, 418) found early precipitation exerted greater influence on forage than other crops. In Colorado, Turner and Klipple (526) reported that blue grama responded quickly to favourable and unfavourable growing conditions and that volume of herbage produced varied widely from year to year. Fults (182) found that moisture conditions were of greater importance than season of year in getting perennial grasses established; and in southern New Mexico, Nelson (340) found that the increase or decrease in area of black grama (Bouteloua eriopoda) was influenced

by the vigour of the plants at the start of the current growing season as reflected by the previous year's precipitation. Current seasonal rainfall had no effect on current density, but it did determine height growth. In the semi-desert grassland of southern Arizona, Lister and Schumacher (274) found that winter rainfall was beneficial to the various species of Aristida but not to Bouteloua rothrockii and B. eriopoda.

In the northern Great Plains, Allred (19) found that the cool season mid grasses and palatable non-grassy herbs are the first plants to go out under heavy grazing and drought. The drought-resistant summer-growing short grasses, dryland sedges, Sandberg bluegrass and unpalatable non-grassy herbs increase during the first stages of depletion of excellent prairie grasslands. Annual grasses and weeds increase with more depletion. Larson and Whitman (272) made a comparison of used and unused badland mesas in the Badlands of South Dakota and concluded that grazing and mowing reduced Stipa and encouraged blue grama.

In Kansas, Riegel et al. (387) compared production of forage grasses on upland, sidehills and lowland and found production on the last was about two and one-half times as much as on the short grass upland. Riegel (386) also compared yields of artificially established grasses and reported that the amount of forage produced per one per cent basal cover of tall grasses was several times greater than that produced by short grasses. Also in western Kansas, Lacey (268) found non-grazed plots produced less herbage than lightly grazed plots, and overgrazing caused an enormous loss in forage production and in ground cover. In the same locality, Tomanek (518) studied five pasture types and found that moderate grazing resulted in more moisture and about twice as much forage as over-utilization. Under light use, there were about equal amounts of blue grama and buffalo grass. With over-utilization, the change was toward all buffalo grass. Aldous (14) has noted the eastward movement of blue grama under the influence of grazing and drought. This is contrasted with weed movement, which according to Gates (188) has been generally westward over a period of 42 years.

Oakley and Westover (344) in 1924 discussed the results from various experiment stations in the northern Great Plains and suggested forage crops and grasses for what they considered the best type of farming -- producing forage and using range for the production of livestock. Fifteen years later, Hoover (231) outlined the characteristics, distribution, forage value, erosion control value, and planting practices for 30 grasses adapted to the Great Plains. In neighbouring Alberta and Saskatchewan, Clarke and Tisdale (108) summarized their investigations including pasture studies, forage crop production, and management of livestock.

In Nebraska, Weaver and Darland (568) transplanted blocks of sod 6 x 6 inches x 4 inches deep from overgrazed and moderately grazed pastures to wooden boxes in the greenhouse. The blocks from the overgrazed pasture produced from 32 to 84 per cent less tops and 28 to 94 per cent less new roots than the grasses in good vigour. In the Texas Panhandle, Caird (89) also found forage yields of blue grama and buffalo grass plants were reduced heavily by overgrazing.

Daubenmire (144) reported that the scablands of the Big Bend area of Washington were badly overgrazed. In near virgin condition, bulk herbage was produced by native perennials, but under heavy grazing, bluegrass and annuals take over what might be called a "biotic climax" of very low production. In southeastern Washington, Daubenmire and Colwell (154) found overgrazing in the Agropyron spicatum-Poa secunda prairie resulted in the removal of tall bunches of Agropyron spicatum and their replacement by dwarf annuals. Resulting directly or indirectly from these vegetational changes caused by overgrazing, there is (1) an increase in the amount of water accumulated in the soil during the winter, (2) a decrease in the aeration of the soil, (3) a reduction of the ability of the soil surface to absorb water, (4) a reduction in the degree of aggregation of soil particles, (5) an increase in the amount of organic matter in the upper decimetre of soil, (6) an increase in the population of bacteria, actinomyces and moulds in the upper decimetre horizon, (7) an increase in the nitrofication power of the microflora, and (8) a decrease in available phosphorus.

In southern Idaho, Craddock and Forsling (138) reported serious depletion from heavy spring and fall grazing by sheep; and Mueggler (330), on the basis of a 25-year study of sheep grazing, concluded:

> 1. Heavy stocking in the fall will not markedly affect grass and forb production; it may cause a decrease in shrubs if they are heavily utilized. 2. Heavy spring stocking will severely reduce grass and forb production and greatly increase the abundance of undesirable shrubs. 3. A range in poor condition will improve very slowly if it is continually grazed in the spring at even a light stocking rate.

In Arizona, Darrow (143) pointed out the relation of various vegetation types to grazing use and some of the changes that have taken place under use, while Humphrey (242) converted the results of his studies in the north central part of the State to guides for recognizing condition and trend of range vegetation. Canfield (96) found that the composition of semi-desert grassland in southern Arizona varies significantly with the general intensity of grazing. He believed that tall, coarse-stemmed grasses such as Arizona cottongrass, sideoats grama and black grama are a part of the climax.

Effects of clipping

Clipping has been used as a means to simulate grazing under controlled conditions, and the results have been used as a guide in studying the effect of grazing. In one such study on prairie sod, Biswell and Weaver (49) found that a direct relation existed between too frequent removal of the tops, deficient root systems, and humus content of the soil. A decrease in humus results in decreased bacterial activity. Plants that are weakened by repeated clippings are less efficient in absorbing water and solutes. They are more subject to damage by drought, disease and to extremes of heat and cold. They extend their area little, or not at all, and compete less vigorously with invaders. Not only is the annual yield of forage reduced, but the life of the plant itself is probably lessened.

Clipping studies conducted by Aldous (12) in two prairie grass pastures near Manhattan, Kansas, showed that yield was inversely proportional to frequency of cutting. Density decreased 60 per cent on plots clipped every two weeks for three seasons. The per cent of protein was highest on plots clipped most frequently, but the total yield was less than on check plots. In western Kansas, Riegel (386) found that clipping closely each four weeks was detrimental to both tall and short grasses. On the basis of clipping studies with bluestem wheat-grass and blue grama, Holscher (230) suggested that some grass should remain ungrazed each year in order to improve the stand. Canfield (95) reported that in the desert grassland of New Mexico close clipping for 11 years practically killed black grama and reduced tobosa (Hilaria mutica) about 60 per cent. On the other hand, Lang and Barnes (270) stated that in southeastern Wyoming short grasses yielded more when harvested frequently at ground or crown level than they did when protected during the growing season and were harvested after growth had ceased. In this connection, Turner and Klipple (526) showed that the air-dry weight of blue grama reached a maximum during the active growth period, then declined as the plants matured. Reductions of 30 per cent were observed during the late summer and fall months. They also noted that blue grama would withstand fairly heavy clipping -- either light clipping at frequent intervals or heavier clipping once during the season.

Blaisdell and Pechanec (54) found that with bluebunch wheat-grass herbage removal was most injurious after substantial regrowth is impossible and before maturity. Similarly, Parker and Sampson (353) obtained smallest yields of two grasses when herbage was removed at the time when growth was at its maximum. In a greenhouse study, Robertson (391) found that frequent clipping of grass seedlings retarded root penetration and reduced yield from 80 to 96 per cent. He observed that clipping reduced growth of roots twice as much as growth of tops. On the basis of water culture studies, Parker and Sampson (353) concluded that a single harvesting resulted in temporary cessation of root growth.

The most important reserve substances of grasses are certain groups of carbohydrates, viz., sugars, fructosans, dextrins, and starch. The type of distribution and relative proportions of reserves vary with the species. Most reserves are accumulated late in the season and are rapidly depleted during early growth in spring; some reserves are used in respiration during winter. Weinmann (576) summarized the yearly cycle by stating that carbohydrates are elaborated in the leaves in excess after flowering and are subsequently translocated to the roots. There they are stored to be drawn on the following spring for the production of new top growth. Evidence was obtained indicating that in autumn nitrogen and phosphorus are translocated from the shoots to the roots in the form of water-soluble substances formed by the breakdown of more complex organic compounds. Storage in stem and leaf bases is important at the end of the season, but much of this material is moved into the roots prior to growth in spring.

Many workers have found the degree of reduction in reserves depended on the time, frequency and closeness of cutting or grazing. Aldous (13), Sampson and McCarty (414), McCarty and Price (297) and others have found that depletion of reserves below a certain critical level may lead to the death of

the plant and, on a large scale, manifests itself in the reduction of basal cover in grasslands subjected to excessive defoliation by cutting or overgrazing. Such decrease is usually associated with an increase in undesirable species of grasses and weeds and paves the way to soil deterioration and erosion.

Graber (194) found that the amount of subterranean and top growth varied inversely with frequency of defoliation and that these defoliated grasses had greater susceptibility to drought, lessened absorptive capacity, and increased winter and insect injury. Benedict (36) reported that lack of nitrogen reduced the total dry weight of Agropyron smithii and Bouteloua gracilis but favoured growth of roots as compared to that of tops. Abundant nitrogen favoured top growth over roots.

The subject of underground development of grasses has been thoroughly reviewed by Weinmann (576). He provided information to show that in most grasses root growth takes place in the cooler seasons. The weight of root systems increases from midsummer to late autumn, usually after shoots have matured and often after herbage growth has ceased. Some grasses renew half or more of their root systems in spring. Stuckey (489) found that in some species the whole root system was regenerated annually with active cell division beginning in October and growth reaching a maximum in April. In other species, only a few new roots were formed after the first spring. Weaver and Zink (571) found that grasses reached their maximum root development in the second or third year, that a large proportion of the roots remained active one to three seasons, and that losses in all species were gradual.

FIRE AS A FACTOR AND AS A TOOL IN LAND MANAGEMENT

Fire as an ecological factor is discussed in the literature under three broad headings: (1) fire as an agent influencing the extent of forests and grasslands, (2) fire as a tool for improving pastures and ranges and (3) fire as a means of eliminating undesirable shrubs and trees.

As the true prairie-forest boundary is in the sub-humid and humid provinces, a discussion of fire as a factor in determining the prairie-forest boundary is outside the scope of this paper. However, fire as a factor in woodland-grassland competition is very important in many places in the arid and semi-arid areas. As Leopold (273) has pointed out, pinon-juniper and oak woodland invaded grassland when fires were eliminated by heavy grazing; Humphrey (241) noted the same for desert shrubs; and Buechner (84) reported that Indians repeatedly burned areas in Kerr County, Texas, to keep trees out. Following white settlement in 1850, the grass areas were changed to a diversified arborescent vegetation, with this vegetation being determined by soils and physiography and the ground vegetation by grazing pressure.

Fire has been used by farmers and ranchers as a means to improve pastures, although the effect of fire is questionable. Hensel (223) burned grass areas in Kansas early each year for four years and reported that his

studies failed to show that burning was injurious. The average yield was slightly greater on the unburned area, but growth was earlier on the burned area. However, Hopkins et al. (233) found that forage production was reduced by more than half by burning. Spring burning was more harmful than fall burning, and the pasture had not recovered after two years. Clarke et al. (109) found that burning mixed prairie in Canada in either spring or fall caused reductions in forage yields, and three to five years were required for complete recovery under moderate grazing. In an annual plant community in California, Hervey (224) noted that on heavily grazed ranges fire had little effect on the proportion of grasses to forbs, but on lightly grazed ranges fire significantly reduced grasses, increased forbs and delayed range readiness. That more than forage may be lost was shown by Elwell et al. (169) in Oklahoma where soil and water losses over a nine-year period were 12 to 31 times more from the burned area than from adjacent woodland.

The use of fire to remove sagebrush is a common practice, but the results may be good or bad according to conditions and to care given the range after burning. This has been shown by Pechanec and Stewart (360) and others. Pickford (363) studied the effects of heavy grazing and burning, separately and together, in an area in Utah where downy brome and sagebrush were practically absent on areas protected from fire and grazing. Heavy grazing resulted in depletion of perennial grasses and an increase in sagebrush and annual grasses. Burning destroyed sagebrush and allowed annual grasses to increase. Under the combined effects of fire and heavy grazing, total density was seriously decreased and annual grasses and poor perennials predominated.

In a review of the literature pertaining to fire in land use and management, Hanson (206) stated:

> ...In many of these practices fire as a tool has proven distinctly serviceable, in some cases it has caused irreparable damage, and in other cases it is doubtful whether the advantages were greater than the disadvantages or not. It is the duty of research to determine fully and accurately the values and losses caused by fire not only to present existing vegetation, animal life, soils, etc., but also to the future conditions of the burned area.

Chaparral burning in California has been the subject of much controversy with full agreement as to the effects of burning yet to be reached. Veihmeyer and Johnston (537) contended that run-off and erosion were not accelerated on burned plots in Shasta and Tehama Counties, while Rowe (398) reported results which showed that burning reduced vegetation to 25 per cent of the original density, and repeated burning decreased infiltration and increased run-off and erosion. On recent burns in the chaparral of southern California, Munns (333) found that up to 90 per cent of the run-off was soil and only 10 per cent was water. The flow of streams on burned areas showed a sharp rise and fall with a relatively low water stage, whereas, on unburned areas, the rise and fall was less steep and there was a longer period of high water.

Sampson (410) also observed that burning and grazing on steep slopes was usually accompanied by accelerated erosion. Burning resulted in increased forage for three seasons, but brush became thicker thereafter. Sampson also noted that burning and overgrazing have widened the chaparral belt because of the strong sprouting habit of the most abundant species, and fire stimulates seed germination. In summing up chaparral burning studies, Sampson (411) stated:

> The burning of a heavy chaparral cover disturbs abruptly the biological and physical equilibrium that existed before the fire. The reaction between the factors favouring the maintenance of a reasonably stable vegetation, and those favouring change in the stability of the soil and the water relations, is accentuated. The degree of change in the habitat will depend chiefly upon climatic factors, character of the vegetation and its rate of regeneration, type of soil and topography. If erosion is the stronger factor, the eventual result will be removal of the top soil, associated perhaps with change in its rate of infiltration and in its water-holding capacity. If, on the other hand, the factors favouring revegetation are the stronger, the area will soon progress to pre-fire conditions, accompanied by geologic normality in soil erosion and perhaps by predictable rates of stream and spring flow.

The whole subject of burning brush ranges has been carefully and objectively reviewed by Shantz (438) who has tried to bring together the various conflicting viewpoints.

PLANT SUCCESSION AS RELATED TO LAND MANAGEMENT

Shantz (437) considered a study of life forms, floristic composition, factors of the habitat, response to the habitat and succession to be important as a basis for recognizing and understanding plant communities. Some writers, notably, Clements (111, 112, 113) and Allred and Edith Clements (20), stressed plant succession. On the other hand, Shreve (463) gave a word of caution in the application of the succession concept to deserts:

> In a consideration of the dynamic aspects of the vegetation of a region in which the initial, sequential and final stages of a succession are characterized by the same species, and often by the same individuals, it is doubtful whether these conceptions, formed in regions with a very dissimilar vegetation, are of much real utility.

Muller (331) made a similar observation for a desert community in Texas. Shreve (452) also noted that changes in vegetation take place slowly. It takes 30 years for the giant cactus to reach a metre in height and 60 years to reach five metres.

The broad successional relations of the arid and semi-arid portions of North America have been covered by a number of investigators (20, 110, 111, 112, 113, 115, 566). In addition, there have been many local successional studies in the arid and semi-arid areas which either related to changes brought about under natural conditions or following disturbances of one kind or another -- cultivation, grazing, fire and drought being the causes most commonly considered. One of the more basic secondary succession studies in the Plains area was that of Shantz (432) in which he outlined the successional stages in the recovery of abandoned roads. To this might be added the study of Booth (64) on algae as pioneers in plant succession. While Booth stressed the place of algae as constituting the initial stage of secondary succession on badly eroded land, his observations showed how important this initial stage can be in increasing infiltration of moisture and reduction of erosion -- two items that are essential in successional development.

In 1919 Sampson (408) applied the concepts of plant succession to range management and opened the way for later studies. Sinclair and Sampson (474) conducted experiments on the establishment and succession of vegetation on different soil horizons. They found that the rate of growth for both annual and perennial species was greater in soil horizon "A" than in horizons of lower depth, regardless of soil or species. Daubenmire (147) compared virgin prairie in southeastern Washington with overgrazed ranges. In virgin prairie, Agropyron spicatum contributed 85 per cent of the forage and Poa secunda and Bromus tectorum five per cent each. Under heavy grazing, Agropyron and Bromus were eliminated, leaving Poa and many small annuals. In the same general locality, Weaver (557) found a direct relation between water content of the soil, the temperature of the soil, the evaporative power of the air and progressive stages in succession. Soil moisture content increased with successional stages, while soil temperature and evaporating power of the air decreased in direct proportion to the advancement of the stage of development. Young (600) found that bluebunch wheat-grass and Idaho fescue were greatly reduced by heavy grazing in the Palouse prairie and were mostly replaced by annual grasses and forbs. On some overgrazed ranges Poa secunda held on but on severely overgrazed areas gave way to Balsamorhiza sagittata and Bromus tectorum. Cottam (133) used historical evidence to show changes in the vegetation of Utah since the arrival of the Mormons. Where grass once covered nearly half the area, it is now replaced by woody types, especially juniper-pinon, sagebrush, rabbitbrush and shadscale, which together increased from 22 per cent of the area in 1847 to 83 per cent in 1937. Cottam and Stewart (134) likewise used historical information to record the changes in Mountain Meadow Valley which was originally made up of wet and dry meadows and is now covered with a dry growth of sagebrush, rabbitbrush and juniper.

Albertson (7, 8) used a background of the vegetational history of the Plains as a basis for the better understanding of recent successional changes caused by grazing and drought, while Dyksterhuis (164) utilized the basic principles of plant succession to develop an objective method for measuring condition and trend on range lands. He observed that under grazing certain species "decrease" while others "increase", and at some stage "invaders" come into the community. By noting these changes and comparing them to known successional standards, it is possible to judge the present stage of development of the range and, by continuing the observations over the years, to

detect the direction of succession. Groh (198) used a little different approach. He found a reduction in the number of species with improvement in productivity and used this change in numbers as a guide to range condition.

The invasion of shrubs on range lands has become a major problem in management, especially in the southern Great Plains and in the desert grassland of the Southwest. In 1908 Cook (127) called attention to the invasion of mesquite and other trees and shrubs in southern Texas. He considered grazing the key factor and believed these woody plants were formerly held in check by fire. Cottle (135) thought that the invasion of desert grassland by "desert scrub" and pinon-juniper woodland was, in the main, the result of breaking the sod and suppressing the grasses by long continued grazing. Where xeric grasses are in possession of the land, they utilize almost the total water supply. Leopold (273) believed the climax in southern Arizona was originally woodland which was held in check by grass competition and fires. Grazing reduced the grass, lowering competition, and there was no fuel to burn; hence, the type is now moving toward the woodland climax.

In the sand dunes of southern New Mexico, Campbell (90) found that the dunes were formed by deterioration of the vegetation and by trampling. If grazing by livestock and rodents is controlled, the area will return to a desert grassland climax. Campbell and Bomberger (92) observed that when Bouteloua eriopoda grassland deteriorates from grazing, drought, or both, the half shrub (Gutierrezia sarothrae) becomes more abundant. It, in turn, may fluctuate with weather conditions and may stay through to the climax. Gardner and Hubbell (185), in a study of an area protected from grazing for eight years, found that Actinea richardsoni, a plant of similar ecological characteristics, decreased in ungrazed and lightly grazed plots. On clay soils, Campbell (91) found that the occurrence and plant composition of each successional stage is determined largely by the type of soil and its associated habitat factors. On sandy clay soils, the climax is mixed Hilaria mutica, Sporobolus brevifolius, and Sporobolus spp.; in dry lake beds, the climax is dominated by Hilaria mutica with Sporobolus airoides on the border.

Haskell (219) observed that Gutierrezia was entirely absent from a lightly grazed pasture in the desert grassland of southern Arizona but comprised about 10 per cent of the shrubby cover on the outside range. He also noted the greater amount of perennial grasses of higher successional rank under the lighter use. In this same area, Beutner and Anderson (43) found that the protection of the soil surface, either by plants themselves or by organic litter which they furnish, prevented sealing of the soil and was of utmost importance in promoting infiltration of water into the soil and in conserving moisture for plant growth. Gardner (183) made a study of an area near Silver City, New Mexico, at an elevation of 5,600 feet after protection from grazing for 30 years. He found that grass densities were about twice as great inside the area as outside.

In the Great Basin and Pacific Northwest, plant succession has received considerable attention. Weaver (555) studied evaporation and plant succession in southeastern Washington; Daubenmire (148) described edaphic, fire and biotic climaxes in southeastern Washington and adjacent Idaho; Eggler (166) made detailed studies on young basaltic flows in southern Idaho;

and Woodbury (593) investigated the biotic relationships of Zion Canyon, Utah, with special attention to succession. Stewart et al. (483) studied changes in the salt desert associations of western Utah and found that grasses and palatable shrubs have decreased and that Chrysothamnus stenophyllus and Russian thistle have invaded. Pechanec and Stewart (361) have used the information derived from successional studies on sagebrush areas as a basis for setting up guides for recognizing condition and trend of vegetation on sagebrush ranges.

Piemeisel (364, 365, 366, 367) has made very careful and detailed studies of the early stages of secondary plant succession in the semi-arid portions of Idaho, Utah and California. He (365, 367) pointed out that the original sagebrush cover in southern Idaho was exceedingly complex. In such a community, the dominant sagebrush has associated with it perennials with bulbs, tuberous roots, and rhizomes, and perennials forming mats, rosettes, tussocks and bunches. Most of the growth is made between the time of fall rains and the beginning of the succeeding hot summer (October to July). Growth is interrupted by winter cold and terminated by summer heat. The annuals that come in following the destruction of the original vegetation grow in spring and summer. The successional order following cultivation is first, Russian thistle; then mustards (Sophia parviflora) or (Norta altissima); and then downy chess (Bromus tectorum). These changes usually take place within five or six years. Grazing by livestock or rodents (366) may result in holding the vegetation in one of these lower stages and retarding or preventing the establishment of native perennials.

Russian thistle, according to Stevens (482), was first observed in the United States in 1873. Wooton (595), in 1895, described its early invasion into New Mexico. In North Dakota, Stevens (482) observed germination usually in April but as late as June. It flowers from June to frost with seeds beginning to develop in August.

Stewart and Hull (484) have recorded the history and spread of Bromus tectorum (cheatgrass or downy chess) in southern Idaho and point out the lower capacity and shorter season of use resulting from the replacement of perennial grasses by this intruder. Hull and Pechanec (238) considered cheatgrass from various angles and weighed its good and bad points. Growing as a winter annual, it is well adapted to climatic conditions in southern Idaho. It often starts in the fall, remains dormant in winter, makes early growth in spring, and is mature and dry by June 5 to 15. Cheatgrass furnishes good soil cover except where burned or too heavily grazed and makes fairly good forage production and fair feed, but it is a high fire hazard. It can be replaced by perennials under management or by reseeding.

Pearse and Woolley (356) found that absorption of surface water is greatly increased under a stand of fibrous-rooted plants. However, Craddock and Pearse (139) found that while wheat-grass is superior in controlling run-off and erosion on steep granitic soils, cheatgrass has considerable erosion control value but is variable from year to year, and it is a high fire hazard. Fire exposes areas to erosion.

Robertson (392) observed in Nevada that sagebrush reduced wind movement, evaporation and soil moisture but increased summer surface soil temperature. Complete removal of brush retarded snow melt. Frischknecht (181), in carrying on experiments leading toward improvement of ranges in the sagebrush zone of central Utah, found that even though fall planting was desirable because it stimulated faster growth and development, winter killing of seedlings was the cause of greatest mortality. Blaisdell (53) reported that reseeded grasses do not compete very successfully with sagebrush seedlings, and the older the sagebrush the less chance there is for grass to become established.

Talbot et al. (493) have called attention to the situation on the 25 million acres of "annual type" grazing land in California where the grassland type, belonging to the California prairie of Clements and Shelford (115), was once largely made up of perennial grasses but now is reduced to three per cent perennials and 58 per cent introduced plants -- the latter mostly from the countries bordering the Mediterranean. The ranges are green only during the winter rainy season and fluctuate abruptly from year to year in quantity and composition of vegetation. Like the cheatgrass ranges mentioned above, they do furnish fairly good forage in season, but the forage value decreases and the fire hazard increases with the onset of the dry season. These alien plants are discussed in detail by Robbins (389). Although they believe much improvement can be made, Bentley and Talbot (40) are of the opinion that there will always be a considerable population of annuals in these California areas.

The various studies of secondary succession following cultivation show the same general trends over most of the Great Plains. Whitman et al. (590) found that in western North Dakota it takes blue grama 40 to 50 years to assume dominance and 40 to 60 years for the return of a complete climax after cover has been destroyed by cultivation. Hutton (243) pointed out that by actual measurement as much as 29 per cent of the total humus has disappeared from the soil at Brookings, South Dakota. Tolstead (514) listed the secondary successional stages in south central South Dakota as: (1) annual forbs, (2) annual and perennial forbs, (3) early perennial grass and (4) climax bunch grass. Costello (131) described essentially the same stages for northeastern Colorado but with a mixed prairie climax consisting of a mixture of short grasses, mid grasses, forbs and shrubs. Where not unduly retarded by grazing or other disturbance, the climax stage is reached in 30 to 60 years. According to Judd (251, 252), recovery was more rapid in Montana and western Nebraska. In the latter locality, *Agropyron smithii* may become important in the fourth year and become the dominating cover in the sixth year. Booth (65) found abandoned fields in east central Kansas had not reached climax prairie conditions in 35 years. Riegel (385), in making a comparison of the rate of recovery for natural and artificial revegetation of retired cultivated land in western Kansas, noted that the area reseeded had about the same grazing capacity in five years as the naturally revegetated pasture had after 15 years. Eby and Whitfield (165) found improvement in the Dalhart sand dune area three and one-half years after stabilization and treatment. Savage (421) estimated abandoned farm land in the southern Great Plains would revert to a good stand of native grass in 25 to 40 years.

BROAD ECOLOGICAL APPLICATIONS

Plant Indicators

Shantz (431) pioneered in the development of the plant indicator concept especially as applied to land capabilities. He noted that in the Great Plains area grama-buffalo-grass land is not the best for crop production. The presence of deep-rooted grasses indicates better conditions, and the wire-grass associations indicate less run-off and deeper moisture penetration. Short grass land is more productive in average or better years, but during drier years, wiregrass land is much the better. This same information, with some additions, was later used by Aldous and Shantz (15) as a basis for setting up the economic significance of vegetation types in the semi-arid portion of the United States. Later, Shantz (436) summarized the available information on plants as soil indicators. In addition to covering soil indicators in considerable detail, he listed plant communities as indicators of growth conditions, temperature, moisture, drought, soil moisture and potential value of land for crops or grazing.

The indicator concept was greatly expanded by Clements (112) who provided comprehensive information covering the entire field of plant indicators. Later, Sampson (409) reviewed the general concept and application of plant indicators. He stated:

> The plant indicator concept is based on a cause-effect relationship, where the effect is taken as a sign of the cause. All plants are admittedly a measure of their environment. Because plant production, and to some extent form of growth, is determined by the habitat, any plant species may, to some extent, indicate the nature of its surroundings; yet only a few key species of a given locality are, as a rule, sufficiently restricted by growth conditions to be helpful.

In this review, Sampson showed how plant indicators have served as a guide in land use as range (pasture) indicators, forest and soil indicators and in chronology. His review is documented with a bibliography of 142 titles.

Kearney _et al._ (255) worked out the indicator significance of vegetation in Tooele Valley, Utah. They found that the sagebrush association grows where soil is rather light in texture, permeable, rather low in moisture-holding capacity and free from an excess of alkali salts, and where, under natural conditions, moisture available for growth is usually exhausted early in the summer.

The _Kochia_ (_Kochia vestita_) association occupies soils of finer texture, lower relative impermeability, higher moisture-holding capacity and a high salt content in the sub-soil. The first foot is usually relatively free from alkali. Moisture is wanting during the summer. The shadscale (_Atriplex confertifolia_) association occupies soils similar to _Kochia_ but these soils frequently contain much gravel and are usually drier and saltier. The greasewood-shadscale association lies between the shadscale and the salt flats.

The soils on which it occurs usually contain more moisture in summer but also are much more saline. The soils of the grass flats (Sporobolus-Distichlis-Chrysothamnus) vegetation are more or less saline and moist to the surface a great part of the year. The salt flat (Allenrolfea-Salicornia) vegetation occupies land which is extremely saline and wet to the surface during a great part of the year. Flowers (176) found similar relations between vegetation and salinity in the Great Salt Lake region. He gives the following alkali tolerances: Salicornia 6 per cent, Suaeda erecta 4 per cent, Allenrolfea 3 per cent, and Distichlis 2 per cent.

Shantz and Piemeisel (441) decided from their studies in the Escalante Valley, Utah, that the most reliable indicators of soil conditions are the stabilized plant associations which are in equilibrium with soil and climatic conditions. Little rabbitbush is an indicator of lighter soils, followed on successively heavier soils by galleta, sagebrush, greasewood, shadscale, winterfat, greasewood-shadscale and saltgrass. Sagebrush and a mixture of sagebrush and greasewood indicate the best land for crops.

In the southern desert area, Shantz and Piemeisel (440) found that probably the best type of land for irrigation agriculture is characterized by a good stand of desert sage. A good stand of creosotebush indicates land which has good drainage and which is free from alkali, but the soil is usually more sandy and not as productive as that occupied by the desert sage. Mesquite and chamiso alone, indicate a very sandy soil free from alkali. Yucca and cactus lands and giant cactus and paloverde lands are too stony or the slope too steep. Seepweed, saltbush, saltbush and arrowweed, pickleweed and saltgrass lands must be leached and usually drained before they will be productive under irrigation.

Daubenmire (145), in setting up the indicator significance of the natural plant communities in the Big Bend area of Washington, listed saltgrass (Distichlis stricta) as an indicator of a harmful degree of alkalinity and high water table for at least a part of the year. Sarcobatus vermiculatus indicates a lower water table and land that can be reclaimed at less cost. Hopsage (Grayia spinosa) indicates mild alkali; Artemisia tridentata, a deep, porous, fertile soil; and Chrysothamnus, a sandy soil subject to blowing.

Meinzer (315) made a very comprehensive study of plants as indicators of ground water. He rated plants as to their reliability as indicators and as to the probable depth of water table indicated. For example, saltgrass is a fairly certain indicator of a shallow water table; Chrysothamnus graveolens is a good indicator of fairly shallow water; mesquite usually indicates water but it may be deep (other writers do not agree); and sacaton (Sporobolus wrightii) may grow where soil is moistened by flood water, or it may indicate shallow ground water.

Talbot (492) used plants as indicators of range conditions, although he considered other criteria in addition. As an example, he states:

> In general, a satisfactory condition of range is indicated by: (1) Vigorous appearance and stand of forage . . . ; (2) absence of accelerated soil washing; (3) lack

of extensive areas overrun by unpalatable plants; (4) slight or no use of unpalatable species; (5) and, on timber-producing areas, absence of serious injury to timber reproduction. Excellent evidence that a previously depleted range is improving includes: (1) thickening of the stand of good forage; and (2) the reclaiming of gullies by vegetation . . . .

Useful plants other than forage

The search for plants that are adapted to arid and semi-arid areas and plants that will produce some product or products on an economic basis goes on continuously. But progress is slow, and sometimes we fail to develop new sources of food, fibre and elastimers because no one person or organization has devoted the time or attention needed to bring promising plants into economic production. Sears (428) has set out very nicely the problems involved in the economic development and use of arid region plants. These include the problems of the physical environment as well as those of the plant to be developed. The answers to these problems are not simple. If they were, they would have been answered long ago.

Several investigators have collected information on useful plants, either presently cultivated, wild, or both. The book Plants Useful to Man by Robbins and Ramaley (390) brings together descriptions of many useful plants, cultivated and otherwise, and it has a good bibliography. Klages' (264) Ecological Crop Geography makes a beginning in assembling information on environmental problems and also provides information on useful crop plants for the semi-arid region. Saunders (419), in his Useful Wild Plants of the United States and Canada, has collected a great deal of interesting information on wild plants under the headings: edible tubers, wild seeds of food value, the acorn as human food, wild fruits and berries, wild plants with edible stems and leaves, beverage plants, substitutes for soap, medicinal wildings and certain poisonous plants. He considered mesquite (Prosopis spp.) the most valuable of wild legumes and recognized the value of other desert plants such as agave, yucca, prickly pear and other cacti. Rose (395), in his notes on useful plants of Mexico, listed many whose range extends into the United States. He gives particular attention to fibre plants and suggested further investigations should be made of the hemp industry with the view of making use of agave plants in western Texas. He also believed that native peppers, fruits, beans, etc., should be tested and more promising ones selected for development. As an example of material to work with, he mentions that 50 species of beans have been reported from Mexico. He believed Agave lechuguilla has promise as a fibre plant. Cruse (142) has prepared an excellent report on his chemurgic survey of the desert flora of the American Southwest. This survey includes plants that might be used for livestock feed, fibre, tannins, oils, candy and other food, wine, etc. He listed the products that might be derived from mesquite, cacti, creosotebush and other plants. He also considered the possible economic use of native plants and pointed out the difficulties, such as slow maturing under desert conditions and the distance from the market.

Information on the possible use of native plants can also be obtained from observing the use that has been, or is being, made of them by the

aborigines. There is rather voluminous literature covering the broad subject of ethnobotany, but much that has been written gives little of definite value. A few of the publications that seem to offer more direct value have been selected for review. Most of these have good bibliographies, so anyone interested can use them as a guide to other publications. Yanovsky (598) has prepared an excellent catalogue of food plants of the North American Indians with references to source of information. This is an excellent reference work with a good bibliography. Whiting's (587) Ethnobotany of the Hopi is one of the better works in this field. He classifies plants by uses and has an annotated list with descriptions of uses. Elmore's (168) Ethnobotany of the Navajo is another good reference. It has a fine set of tables and a good bibliography. The pinon nut is cited as an example of a plant product used by Indians that has been exploited commercially. The notes and tables in this publication would be valuable for anyone wanting to develop new plants for arid regions. Collins (123) has written up the drought-resisting maize cultivated by the Hopis. The varieties of maize grown by them and other agricultural Indians have two special adaptations: (1) a greatly elongated mesocotyl that permits deep planting, and (2) the development of a single large radicle that rapidly descends to the moist sub-soil and supplies water during the critical seedling stage. These are not just inferior varieties of "squaw corn" but some compare well in production to improved varieties. The peculiar adaptations of this type of corn definitely indicate its value for semi-arid regions.

Castetter and Bell (103) have written a comprehensive treatise on Pima and Papago Indian agriculture that tells how these agriculturally inclined Indians have maintained an existence in an arid region. These Indians live in the Sonoran Desert where the average rainfall is 10 inches or less - a land of hot summers, mild winters, and wide daily range of temperatures. They rely, to a considerable extent, on native plants. They use the fruits of the sahuaro (Cereus), cholla and prickly pear (Opuntia spp.), mesquite (Prosopis) fruit and seed, mescal (Agave spp.), and the datil (fruit of Yucca baccata). They also obtain greens from Amaranthus spp., Chenopodium spp., and saltbushes (Atriplex spp.). Their principal native crops are maize, beans and pumpkins.

Rubber plants have been given more consideration for development than any other plant of the arid areas of the United States. Of the rubber plants, guayule has been exploited the most. It has been harvested from its native habitat in Mexico to almost complete extinction. In the United States, it has been under experimental and limited commercial cultivation for over a period of 50 years; and it has been carried to other arid regions throughout the world. The status of guayule production was reviewed by Whaley (583) in 1948 and, more recently, by Taylor (495) who gives a splendid picture of the past and recent developments in bringing guayule into a position for economic production. On a world-wide basis, there is a large area that is suited to guayule production. It could be grown on three million acres in Texas and on several thousand in Arizona. Guayule is being grown in Turkey and in Spain, and there is reason to believe that it is being grown in Russia. Processing methods have been worked out for extracting a high quality rubber that can be used for manufacturing articles for which natural rubber is needed.

Other rubber-producing plants have been investigated, and although some show promise, none of those growing in the arid parts of North America measure up to guayule (583). In 1919 Hall and Goodspeed (200) made a rubber plant survey of western North America and found rubber of high grade in the genus Chrysothamnus, but the percentage was low and the rubber difficult to extract. Polhamus (371) investigated the rubber content of various species of goldenrod and found a significant amount of rubber in the leaves but none in the other plant parts. It, too, was difficult to extract. G. Whiting (588) has reviewed the work on milkweeds (Asclepias), and she shows that the desert species have the most promise for rubber production, but the rubber is of low quality. She also points out that milkweeds are valuable for fibre and oil. Buehrer and Benson (85) made a survey of 93 genera of southwestern desert plants. Most of these have very little, if any, rubber.

For those desiring additional information on rubber-producing plants, Moyle (329) has prepared a very complete bibliography with abstracts of publications.

Next to rubber plants, potential producers of fibre products have received the most attention in the arid Southwest. Greene (196) compared the fibre and waste of Agave lechuguilla with A. americana and noted their similarities but could see no commercial use at that time (1932). Cruse (142) agreed with Greene in general and reported no commercial use of agave in 1949. Botkin et al. (68) investigated the distribution and yield of Yucca glauca, Y. elata, and Nolina spp., and found these potential fibre-producing plants occurred naturally in commercial quantities and could be used in an emergency. They reported that yucca fibres were equal in strength to hemp and Manila (hemp) fibres and stronger than Nolina fibres which are about equal to sisal, jute and raw silk, but they were stronger than cotton and linen fibres. Botkin and Shires (67) tested fibres from various species of yucca and found they compared favourably in tensile strength and other qualities with commercial fibres. The fibres are white and lustrous and are suitable for making twine, burlap, rope, special kinds of hard-fibre paper and soft brushes. Bell and Castetter (35) delved into the utilization of yucca, sotol and beargrass by the aborigines of the southwestern United States Fibre from the leaves was the most important product obtained. It was used for tying and was woven into nets and fabrics. The root, and occasionally the whole plant, yielded saponaceous ingredients used as a detergent. The fleshy-fruited Yucca baccata and the crowns of sotol (Dasylirion) were used for food.

In terms of economic production, the slow growth of yuccas and agaves is a serious drawback. That yucca grows slowly has been shown by Campbell and Keller (94) who found that Yucca elata grows an inch a year. The new leaves grow rapidly during the summer, droop the second or third year, and die the fourth year. The dead leaves persist many years.

Of the trees and shrubs, mesquite (Prosopis spp.) has been given the most consideration for possible commercial use. In 1895 Forbes (177) pointed out that the mesquite tree affords small sizes of handsome, durable wood; the fuel is of high value, and it makes an excellent charcoal. The abundant gum has industrial and medicinal value, the beans make good forage,

the flowers are a source of honey, and the entire tree contains tannic acid. Mell (316) supported Forbes' appraisal and added that the wood is used as a substitute for mahogany for small turned articles and for exposed timbers such as posts, ties and timbers in buildings. He also reported that some mesquite wood is shipped from Mexico to United States markets where it is sold by the ton. Shinn (446) has reported on the possible uses of the exotic acacias, but it seems that very little attention has been given to the possible culture of native species. It is quite possible that gums, perfumes and tannin might be derived from some of the native trees. However, the smaller size of our species might be a disadvantage.

Mirov (325) summed up the available information on the jojoba (Simmondsia) indicating that it has considerable promise for wax production. Simmondsia grows in abundance in Arizona and adjacent parts of Mexico, occupying an area roughly 700 miles long and 100 miles wide. The dioecious plants produce seeds about the size of peanuts which the Indians roast for food or boil in water to extract the oil. The early Spanish thought the oil had medicinal qualities. Chemically, the material is wax rather than oil and has properties similar to sperm oil. When hydrogenated, it makes a very hard wax. Because it is not digested, it could be used in a non-fattening salad dressing.

Rabak (376) made a study of plants producing essential oils that might have commercial value. The native plants tried thus far are mostly from humid and sub-humid areas. It is possible that some plants from semi-arid and arid regions may be of value and also that some introduced plants might well be grown in arid and semi-arid regions. Methods of extraction and purification were also considered by Rabak.

Buehrer et al. (86) made a careful investigation of the chemical composition of rayless goldenrod (Aplopappus Hartwegi) and found a variety of ingredients that might have commercial value. It contains an unusually high percentage of resins, up to 25 per cent in the leaves with an average of 8 per cent for the plant. Essential oils and alkaloids of possible value were also found.

As a source of tannin, canaigre, a species of Rumex, was given considerable attention around the turn of the century. Forbes (178) found the tannin from canaigre to be very good, especially for the production of patent or enamelled leathers; also for sole and harness and for light leathers. He found canaigre was relatively easy to grow and a good producer. Hare (213) reported crops of ten tons to the acre. The roots have from 15 to 42 per cent tannin, and best results are obtained when the crop is harvested every two years. Canaigre is unable to stand much frost.

Cacti, mostly species of Opuntia, have been given a great deal of attention but have not worked out very well on a commercial basis. They are rather slow growing, and the products that might be derived from them can be obtained more efficiently from other sources. This fact has been pointed out by Wooton (596) who made a rather exhaustive study of prickly pears and other Opuntias. His conclusions were that as a stockfeed, production is very limited, and that the highly advertised spineless varieties winterkill even in the warmest parts of New Mexico. The fruits (tunas) are used by the Spanish-Americans, but the New Mexico varieties are not as good as those found in Mexico.

Griffiths and Thompson (197) prepared a comprehensive report in 1929 covering the propagation, culture, diseases, insect pests and economic value as a source of fruits, wood, medicines, cactus candy and also its possible use for hedges and decorative purposes. They, too, could see no great promise for the exploitation of cacti.

Members of the genus Atriplex and close relatives have been given consideration during the past years as plants that could be grown for forage production on saline soils. In 1900 Kennedy (260) gathered information on 40 species belonging to the genus Atriplex in the Western States and described their growth habits, characteristics and possible economic uses. Twenty-five years later, Bidwell and Wooton (44) brought up to date the information on saltbushes giving descriptions, distribution, and information on their chemical analysis. The saltbushes, although valuable in their native habitats, have not shown too much promise under cultivation.

In addition to the papers discussed above, some of the more general publications covering groups of plants furnish some information on the economic uses of native plants. Among those of more than passing interest are: Dayton (155), Little (275) and van Dersal (533).

Afforestation

Planting trees and shrubs for protection of one kind or another has been going on for a long time. The control of sand dunes by planting was a well-developed art (228) in the latter part of the nineteenth century. The afforestation of the sand hills, in Nebraska especially and elsewhere in the Plains, got under way early in the twentieth century (30).

Gates (187) noted that pine groves, probably planted by the early settlers in the 1890's, were still maintaining themselves in the early 1920's. However, Albertson and Weaver (10) found these suffered heavy losses in the 1930's. Gates observed that the groves were eliminating prairie plants within the groves but were not invading the grassland. The trees produced viable seed, but the seedlings could not get established. Fire was the greatest enemy to survival and extension. In Oklahoma, Harper (214) found that success of tree growth depended upon the percent of clay and on other soil structure characteristics. Niederhof and Stahelin (342) studied climatic conditions within and adjacent to a 36-year old forest plantation in the Nebraska sand hills and found that wind movement inside was only 28 per cent and evaporation 58 per cent of that in the open.

The value and influence of windbreaks were set forth by Bates (29) in 1911. He noted that the protective value of an osage-orange hedge was equal to the yield of a strip twice as wide as the height of the trees, and the protection from the most efficient grove amounted to three times as wide as the height of the trees. In Canada, Ross (397) considered that the protection afforded by shelter-belts was in the ratio of 50 feet for every foot of height growth. He found that the compact soils of the prairie required especial treatment to get trees started. Under newly broken sod, thorough cultivation and summer fallow were necessary; on cultivated land, the soil might be looser and less culture was required. His report also gives recommendations as to species and methods of planting and care.

In studies at Havre, Montana, Harrington and Morgan (215) found that summer fallow the year preceding planting was beneficial. Under climatic conditions with annual precipitation of 13.80 inches and range in temperature from -40° to 104° F., they recommended the following species: American elm, Chinese elm, green ash, boxelder, jack pine, yellow pine, spruce and caragana. At the Judith Basin Branch Station in Montana, where the annual precipitation is under nine inches, Jensen and Harrington (249) believed summer fallow before planting was essential, and they limited recommended species to caragana, boxelder, green ash, American elm, Chinese elm and Russian olive.

In the drought depression years of the early and middle 1930's, a study of the whole shelter-belt situation was made by a group of scientists under the auspices of the United States Forest Service (4, 220, 530). This review of conditions, including climate, soils, vegetation, economic and social aspects, and experiences in tree-planting in other lands, was used as a basis for the extensive Prairie States forestry programme carried out during the following years. The success of this programme was evaluated some 10 years later by Munns and Stoeckler (334). They sampled the 19,000 miles of belts planted on 33,000 farms between 1934 and 1943 and found 78.4 per cent of the plantings rated good or better and 10.4 per cent were unsatisfactory. Ponderosa pine showed the poorest survival (39.2 per cent) and boxelder the best (85.0 per cent). Growth rate was 30 to 50 per cent greater in areas of better rainfall than in arid portions of the shelter-belt zone. Best planting sites were generally the deep sandy loam or loamy sand soils with deep moisture penetration. There was a striking difference in growth rate and survival in favour of sandy, as opposed to heavy, soils for many species. The chief causes of unsatisfactory conditions were: inadequate cultivation for the first four years, grazing, insects, diseases, rodent pests and some damage from hail and snow. The tall-growing species - white willow, boxelder, ailanthus, honey locust and black locust - made the best growth. The most successful conifers were Ashe juniper, jack pine, eastern red cedar, Scotch pine and Rocky Mountain juniper; and the best shrubs were Tatarian honeysuckle, sand plum, caragana, American plum and golden willow.

Over a period of twenty years, Ross (396) made a similar study of the results from tree planting in the prairie provinces of Canada. He considered the best species to be Manitoba maple, green ash, caragana, Russian poplar and Russian willow. The native elm is very good, but rabbits mow it down. Cottonwood usually died within five to ten years. The native white spruce, jack pine, lodgepole pine and hardy strains of Scotch pine were the best of the conifers. Ross favours close spacing (4' x 4') as giving better results with less labour than wider spacing.

George (189) reported on the growth and survival of deciduous trees in a series of 22 shelter-belt combinations at Mandan, North Dakota. During the period 1915-1934, precipitation averaged 15 inches, and the recorded temperature extremes were -43° and 110° F. All poplar, willow and birch species showed heavy killing back and heavy mortality during the period. Chinese elm, green ash, boxelder, chokecherry, Siberian pea-tree, buffaloberry and American plum maintained satisfactory growth. Results from spacing tests

were not conclusive, but George preferred a spacing that would eventually give forest conditions. Munns and Stoeckler (334) agreed and noted that most shelter-belts five to ten years old had closed in and had a leaf mulch one-half to one inch deep. Jensen and Harrington (249) and Harrington and Morgan (215) preferred spacing that would allow clean cultivation. This controversy as to what is the best spacing is still not settled.

Daubenmire (152) has summed up his observations on afforestation problems in arid North America by pointing out that drought has proved to be the key factor. Success depends upon the degree to which advantage is taken of (1) coarse soils which favour deep-rooted trees, (2) depressions in topography which slightly increase available moisture and decrease transpiration, (3) slopes directed away from sun and wind, and (4) avoidance of soils with high salinity, calcium, carbonate, etc.

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Publications pertaining to plant geography in Canada and Alaska have been exhaustively covered in a series of publications by Adams (2) and Senn (429) and their associates. Renner et al. (382) covered publications in range management and related fields (including ecology) prior to 1938. Arctowski (21) compiled a bibliography on climatic variations that is very useful. The bibliographies in botany for Colorado by Allison (17) and for Arizona by Ewan (173) are helpful in those States.

KEY TO ABBREVIATIONS

USED IN

THE BIBLIOGRAPHY

Acad. . . . . Academy
Agric.. . . . . Agriculture, Agricultural
Agron.. . . . . Agronomy
Agros.. . . . . Agrostology
Amer. . . . . America, American
Ann.. . . . . Annals, Annual
Assoc.. . . . . Association

Biol. . . . . Biology, Biological
Bot.. . . . . Botany, Botanical
Bull. . . . . Bulletin
Bur.. . . . . Bureau

Can.. . . . . Canada
Canad.. . . . . Canadian
Circ. . . . . Circular
Congr.. . . . . Congress
Conserv.. . . . . . . Conservation
Contrib.. . . . . . . Contributions

Dept. . . . . Department
Div.. . . . . Division

Ecol. . . . . Ecology, Ecological
Econ. . . . . Economic
Ed. . . . . Edited, Edition
Ent.. . . . . Entomology
Exp.. . . . . Experiment

For.. . . . . Forest, Forestry

Gaz.. . . . . Gazette
Geogr.. . . . . Geography, Geographers, Geographical
Geol. . . . . Geology, Geological
Geophys.. . . . . . . Geophysical
Govt. . . . . Government
Gt. Brit. . . . . . . Great Britain

Hort. . . . . Horticultural

Indus. . . . . Industry
Inst. . . . . Institute, Institution
Int. . . . . Interior
Internatl. . . . . . International

Jour. . . . . Journal

Manag. . . . . Management
Misc. . . . . Miscellaneous
Monog. . . . . Monographs

Natl. . . . . National
Nat. . . . . Natural, Naturalist
No. . . . . North, Number

Physiol. . . . . . . Physiology, Physiological
Pl. . . . . Plant
Proc. . . . . Proceedings
Publ. . . . . Publication

Rpt. . . . . Report
Res. . . . . Research, Researches
Rev. . . . . Review, Revised

Sci. . . . . Science, Sciences
Scient. . . . . . . Scientific
Ser. . . . . Series
Serv. . . . . Service
Soc. . . . . Society
St. . . . . State
Sta. . . . . Station
Stud. . . . . Studies
Surv. . . . . Survey

Tech. . . . . Technical
Trans. . . . . Transactions

U. S. . . . . United States
Univ. . . . . University

Wash. . . . . Washington

Zool. . . . . Zoology

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